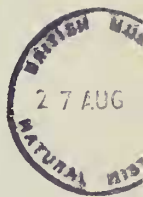


CERTAIN PALAEONISCOID FISHES AND THE  
EVOLUTION OF THE SNOUT IN  
ACTINOPTERYGIANS



BY

BRIAN GEORGE GARDINER, Ph. D.  
(Queen Elizabeth College, University of London)

*Pp. 255-325; 2 Plates; 20 Text-figures*

BULLETIN OF  
THE BRITISH MUSEUM (NATURAL HISTORY)  
GEOLOGY

Vol. 8 No. 6

LONDON: 1963

THE BULLETIN OF THE BRITISH MUSEUM  
(NATURAL HISTORY), *instituted in 1949, is  
issued in five series corresponding to the Departments  
of the Museum, and an Historical series.*

*Parts will appear at irregular intervals as they  
become ready. Volumes will contain about three or  
four hundred pages, and will not necessarily be  
completed within one calendar year.*

*This paper is Vol. 8, No. 6 of the Geological  
(Palaeontological) series. The abbreviated titles of  
periodicals cited follow those of the World List of  
Scientific Periodicals.*

© Trustees of the British Museum 1963

PRINTED BY ORDER OF THE TRUSTEES OF  
THE BRITISH MUSEUM

*Issued July, 1963*

*Price Twenty Shillings*

# CERTAIN PALAEONISCOID FISHES AND THE EVOLUTION OF THE SNOOT IN ACTINOPTERYGIANS

By B. G. GARDINER

## CONTENTS

	<i>Page</i>
I. INTRODUCTION . . . . .	258
II. SYSTEMATIC DESCRIPTIONS . . . . .	259
Order PALAEONISCIFORMES	
Sub-order Palaeoniscoidei	
Family ELONICHTHYIDAE Aldinger . . . . .	259
Genus <i>Elonichthys</i> Giebel . . . . .	259
Family COSMOPTYCHIDAE nov. . . . .	259
Genus <i>Watsonichthys</i> Aldinger . . . . .	260
<i>Watsonichthys pectinatus</i> (Traquair) . . . . .	260
Genus <i>Cosmoptychius</i> Traquair . . . . .	265
<i>Cosmoptychius striatus</i> (Agassiz) . . . . .	266
Family ACROLEPIDAE Aldinger . . . . .	271
Genus <i>Mesonichthys</i> nov. . . . .	271
<i>Mesonichthys aitheni</i> (Traquair) . . . . .	272
Family PYGOPTERIDAE Aldinger . . . . .	276
Genus <i>Nematoptychius</i> Traquair . . . . .	276
<i>Nematoptychius greenocki</i> (Traquair) . . . . .	276
Family RHABDOLEPIDAE nov. . . . .	284
Genus <i>Rhabdolepis</i> Troschel . . . . .	284
<i>Rhabdolepis macropterus</i> (Bronn) . . . . .	285
<i>Rhabdolepis saarbrueckensis</i> n. sp. . . . .	289
Family AMBLYPTERIDAE Romer . . . . .	290
Genus <i>Amblypterus</i> Agassiz . . . . .	290
<i>Amblypterus latus</i> Agassiz . . . . .	291
Family STEGOTRACHELIDAE nov. . . . .	294
Genus <i>Stegotrachelus</i> Woodward & White . . . . .	294
<i>Stegotrachelus finlayi</i> Woodward & White . . . . .	295
Genus <i>Moythomasia</i> Gross . . . . .	297
<i>Moythomasia devonica</i> (Clarke) . . . . .	297
<i>Moythomasia antiqua</i> (Williams) . . . . .	298
Family TEGEOLEPIDAE Romer . . . . .	299
Genus <i>Tegeolepis</i> Miller . . . . .	299
<i>Tegeolepis clarki</i> (Newberry) . . . . .	300
Family CHEIROLEPIDAE Pander . . . . .	303
Genus <i>Cheirolepis</i> Agassiz . . . . .	303
<i>Cheirolepis trailli</i> Agassiz . . . . .	303
<i>Cheirolepis canadensis</i> Whiteaves . . . . .	306
III. DISCUSSION . . . . .	307
The snout region in actinopterygians . . . . .	307
IV. SUMMARY . . . . .	318
V. ACKNOWLEDGMENTS . . . . .	319
VI. REFERENCES . . . . .	319
VII. LETTERING USED IN TEXT FIGURES . . . . .	324

## SYNOPSIS

A redescription is given of the type species of the genera *Watsonichthys* Aldinger, *Cosmoptychius* Traquair, *Nematoptychius* Traquair and *Mesonichthys* *gen. nov.* from the British Carboniferous, supplemented by an account of members of the Devonian genera *Stegotrachelus* Woodward and White, *Moythomasia* Gross, *Tegeolepis* Miller and *Cheirolepis* Agassiz, and the Permian *Rhabdolepis* Troschel and *Amblypterus* Agassiz. These genera are placed in appropriate families, and the evolution of the snout region in actinopterygians is discussed.

## I. INTRODUCTION

THE British Carboniferous strata have yielded a vast array of palaeoniscoids. A few of these, nine in all, were described by Agassiz as long ago as 1843, but the main contribution to our knowledge of these forms was given by Traquair (1877-1914) in his monograph on "The Ganoid fishes of the British Carboniferous formations". More recently Moy-Thomas and Dyne (1938) have redescribed the Lower Carboniferous palaeoniscoid fauna from Glencartholm, Eskdale, in an attempt to supplement those descriptions already given by Traquair (1877-1914). Apart from these accounts, the only other real contribution has come from White (1927, 1937 and 1939) who has described several new Carboniferous genera.

This paper is intended to be the beginning of a revision of all the genera described by Traquair (1877-1914) with the exclusion of those genera adequately redefined by Moy-Thomas & Dyne (1938). This work is mainly concerned with redefining selected genera, and to that end only the type species are dealt with. In subsequent papers it is hoped to redefine the remaining Carboniferous genera, and then to examine the vast array of species which have been included within them. This is only possible when adequate generic descriptions are available. Needless to say, any such study is supplemented by digressions on the part of the writer into descriptions of genera other than Carboniferous where they are of interest to him and to the evolutionary picture as a whole. Thus I have redescribed several Devonian and two essentially Permian genera.

Some attempt is made at classification into families, although their relationships to one another are not dealt with exhaustively at this stage.

In the course of this work the problem of the snout region in the palaeoniscoids has become somewhat clearer and the main contribution made in the discussion is an effort to elucidate the evolution of the actinopterygian snout.

The following letters indicate some of the Museums from which specimens were borrowed :—

A.M.N.H. American Museum of Natural History, New York.

B.M.N.H. British Museum (Natural History), London.

R.S.M. The Royal Scottish Museum, Edinburgh.

U.M.Z.C. University Museum of Zoology, Cambridge.



## II. SYSTEMATIC DESCRIPTIONS

Order **PALAEONISCIFORMES**Sub-order **PALAEONISCOIDEI**Family **ELONICHTHYIDAE** Aldinger, 1937 : 16

DIAGNOSIS. See Aldinger, 1937 : 16, 204.

Genus **ELONICHTHYS** Giebel, 1848

DIAGNOSIS (emended). Body fusiform ; fins large with small fulcra anteriorly and lepidotrichia distally bifurcated. Dorsal and anal fins triangular and of much the same size, dorsal fin opposed to the space between pelvic and anal fins ; pectoral fin with rays jointed to their base, and pelvics short based ; anal fin triangular, without fringe, similar in shape to pelvics, caudal fin deeply cleft and inequilateral. Skull with well-developed rostrum, oblique suspensorium and medium-sized orbit ; opercular larger than subopercular, with antero-dorsal dermohyal, but no ventral accessory bone in opercular series ; suborbitals present, and row of supraorbitals between dermosphenotic and nasal bones. Branchiostegal rays numerous, teeth acutely conical and arranged in two series—inner row of well spaced, large laniaries and outer row of numerous, closely arranged teeth. Scales rhomboidal, often denticulated posteriorly, large ridge scales in front of median fins. Skull bones ornamented with tuberculations and striae of enamel.

TYPE SPECIES. *Elonichthys germari* Giebel.

REMARKS. It has been found necessary at the outset to redefine the genus *Elonichthys* Giebel in order that the genera dealt with in this paper may be more clearly separated from it, since most of them have at some time or another been included in the genus *Elonichthys*.

Family **COSMOPTYCHIIDAE** nov.

DIAGNOSIS. Body fusiform, dorsal fin arising well in front of anal fin, both fins triangular. Caudal fin deeply cleft, heterocercal and inequilateral. Pectoral fin with bases of principal rays unjointed, and pelvics long based. All fins with numerous small fulcra anteriorly and lepidotrichia distally bifurcated. Skull rounded anteriorly and without well-developed rostrum. Suspensorium oblique and orbit large. Antorbital bears teeth. Opercular much larger than subopercular with antero-dorsal dermohyal and antero-ventral accessory opercular. Branchiostegal rays numerous and suborbital series present. Scales rhomboidal with pronounced striae. Dentition consisting of a series of large laniaries flanked on outside by series of more numerous, smaller teeth.

REMARKS. I have erected this family to include the two Lower Carboniferous genera, *Watsonichthys* Aldinger and *Cosmoptychius* Traquair. These two genera show many resemblances, of which the single accessory opercular and the long based pelvics are probably the most significant.

This family is closely allied to Aldinger's (1937 : 376) group A of the family Acrolepididae and in fact is probably ancestral to this group. For example, the scale structure of *Watsonichthys* is very much that of the Acrolepid-type (Aldinger, 1937 : 257) and both *Plegmolepis* Aldinger and *Acropholis* Aldinger have accessory operculars.

### Genus *WATSONICHTHYS* Aldinger, 1937

1877a *Elonichthys* Traquair, *partim*, p. 430.

DIAGNOSIS (emended). Body fusiform ; dorsal fin arising well in front of anal, both fins triangular, but anal much extended and fringe-like in hinder half ; caudal fin deeply cleft and inequilobate ; pectoral fin with principal rays unjointed in proximal third of their length, pelvics long based ; all fins with numerous small fulcra anteriorly and lepidotrichia distally bifurcated. Skull without well-developed rostrum and with two pairs of extrascapulars, suspensorium oblique and orbit medium-sized with a sclerotic ring ; opercular much larger than subopercular with antero-dorsal dermohyal and antero-ventral accessory opercular, branchiostegal rays numerous, suborbitals present ; cranial roof bones and cheek bones ornamented with tubercles and ridges of enamel ; teeth consisting of well-formed, conical lanianaries and numerous smaller teeth ; scales rhomboidal with pronounced striae.

TYPE SPECIES. *Elonichthys pectinatus* Traquair.

REMARKS. When Aldinger erected this genus to incorporate *Watsonichthys pectinatus* (Traquair) he also tentatively included in it *Watsonichthys* (?) *aitkeni* (Traquair). However, as I shall show later in this paper, *Watsonichthys* (?) *aitkeni* does not in fact belong to the genus *Watsonichthys*.

There is one other species, *Watsonichthys lotzi* (Gürich) from the Upper Dwyka Shales of Ganikobis, South Africa, which appears to be a member of this genus (Gardiner, 1962).

### *Watsonichthys pectinatus* (Traquair) (Text-fig. 1)

- 1877a *Elonichthys* (?) *pectinatus* Traquair, p. 430.
- 1879 *Elonichthys pectinatus* Traquair : Traquair, p. 121.
- 1882 *Elonichthys pectinatus* Traquair : Traquair, p. 545.
- 1887 *Elonichthys pectinatus* Traquair : Traquair, p. 315.
- 1891 *Elonichthys pectinatus* Traquair : Woodward, p. 500.
- 1897 *Elonichthys pectinatus* Traquair : Traquair, p. 144 (name only).
- 1901 *Elonichthys pectinatus* Traquair : Traquair, pp. 82-87, text-fig. 1, pls. 13, 14, figs. 1-3.
- 1921 *Elonichthys pectinatus* Traquair : Stensiö, p. 219.
- 1925 *Elonichthys pectinatus* Traquair : Watson, pp. 851-853, text-fig. 21.
- 1937 *Watsonichthys pectinatus* (Traquair) Aldinger, pp. 207, 254-257, text-fig. 72.
- 1938 *Elonichthys pectinatus* Traquair : Moy-Thomas & Dyne, p. 462.
- 1954 *Elonichthys pectinatus* Traquair : Waterston, p. 64.

DIAGNOSIS (emended). A large species reaching almost one metre in length. Body fusiform and anal fin with distinct fringe posteriorly. See also Traquair, 1901 : 82.

HOLOTYPE. Scales, R.S.M. 1874.22.2, and counterpart from the Gilmerton Ironstone, Gilmerton, near Edinburgh, Lower Carboniferous Limestone Series.

MATERIAL. Specimens including the holotype from the Royal Scottish Museum and from the British Museum (Nat. Hist.). Approximately thirty specimens were examined, twelve of which showed well preserved skulls.

REMARKS. This species was included in the genus *Elonichthys* Giebel by both Traquair and Woodward, but Aldinger (1937 : 254) placed it in a new genus, *Watsonichthys*, because of the several differences he believed it showed from the genus *Elonichthys*. These differences are quite apparent, especially the pectoral fin with its unjointed lepidotrichia and the fringe to the anal fin, not to mention the opercular apparatus. The question of the opercular apparatus is not so clear, Traquair (1890 : 397) considers the presence of a ventral accessory bone ("Y") in front of the opercular to be quite a common feature of the genus *Elonichthys*. However, the type species *Elonichthys germari* Giebel, as far as I can judge, does not possess this accessory bone, neither do *Elonichthys serratus* Traquair or *Elonichthys pulcherrimus* Traquair (Moy-Thomas & Dyne, 1938, text-figs. 22-25). The species of *Elonichthys* which allegedly possess this accessory bone, *Elonichthys pectinatus* Traquair and *Elonichthys striatus* (Agassiz), are undoubtedly members of other genera and as such can be removed, *E. pectinatus* Traquair being placed in the genus *Watsonichthys* Aldinger (1937), and *E. striatus* (Agassiz) in the genus *Cosmoptychius* Traquair (1877) See p. 266. Thus if we amend the definition of the genus *Elonichthys* Giebel given by Aldinger (1937 : 16) to include the two following facts, first that the anal fin is triangular and without a fringe and second, that there is no ventral accessory bone in the opercular series (See p. 263), then it is quite clear that Aldinger was perfectly justified in erecting the genus *Watsonichthys* to include *Watsonichthys pectinatus* (Traquair).

DESCRIPTION. *The skull.* The general shape of the skull can be seen from Text-fig. 1. The snout is rounded and not produced into a rostrum as in the genus *Elonichthys* Giebel. The external bones of the skull are all strongly ornamented with tubercles and ridges of enamel. The extrascapulars, parietals and frontals are ornamented with tubercles which tend to become confluent, forming short ridges, and which follow the length of the bone. The ridges of enamel on the dermopterotics are somewhat longer. The infraorbitals and suborbitals are mainly covered by tubercles and a few short striae. The maxilla has tuberculations along its ventral margin, but the expanded part is ornamented by ridges and lines of tubercles running parallel with the dorsal and posterior margins. On the pre-opercular the tubercles follow the posterior margin. The opercular, subopercular, accessory opercular and dermohyal are all uniformly ornamented with tubercles and short striae which run concentrically round the bones. The tubercles on these opercular bones are often pointed and are invariably striated with delicate grooves which converge towards the apex of the tubercle and in this respect are similar to those found on the dermopterotics. The ornamentation of the lower jaw consists of short stout ridges of enamel which are sinuous, occasionally branched and which

more or less follow the length of the jaw. Interspersed among the ridges are more pointed tubercles. The ridges are characterized by delicate striae, similar to those described on the tubercles, which run from the grooves up to the crest of the ridge on both sides, giving a herring-bone appearance to the ridge when viewed from above. The branchiostegal rays are more delicately ornamented with ridges and tubercles, the tubercles often being striated.

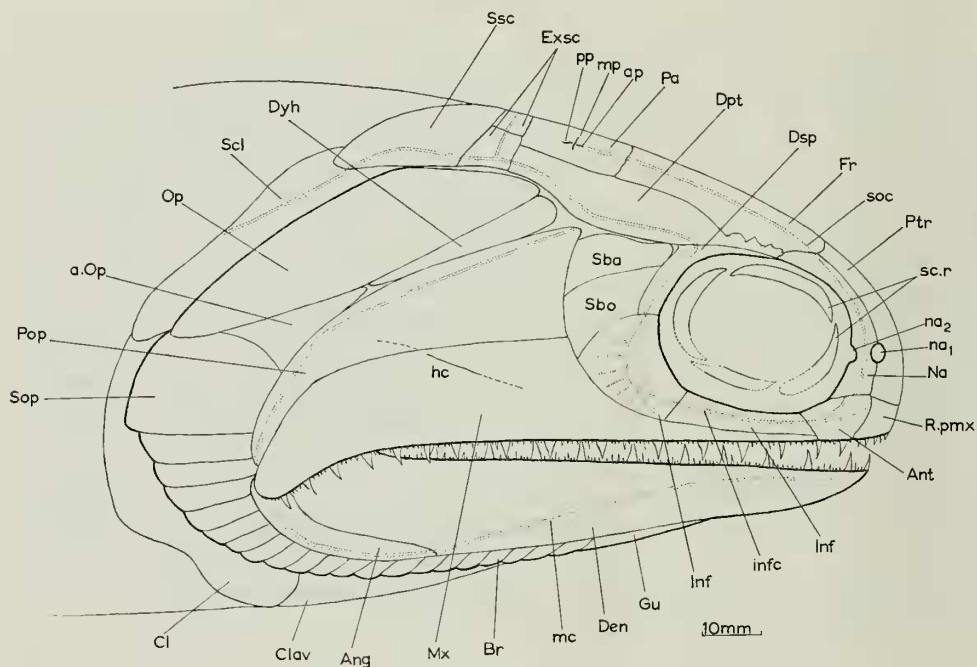


FIG. 1. *Watsonichthys pectinatus* (Traquair). Restoration of skull in lateral view.

The skull of *Watsonichthys* is long, with an oblique suspensorium and the orbit situated well forward. The large suprascapulars are joined to two pairs of extrascapulars anteriorly. The median pair of extrascapulars is small and square, while the members of the outer pair are larger and more rectangular. The parietals are quite large in this species and all three pit lines are clearly visible on them. The frontals are somewhat expanded anteriorly and the antero-lateral edge which joins the anterior margin of the dermopterotic has a characteristic wavy suture (R.S.M. 1896.34.1, 1896.34.2). Anteriorly the frontals meet the median postrostral and the nasals. The dermopterotic is a very long ossification which anteriorly just comes into contact with the most posterior edge of the nasal and extends the lateral edge of the skull roof quite considerably. The nasals and postrostral curve downwards to give the snout a rounded shape which can be clearly seen in a relatively uncrushed specimen preserved in the round (B.M.N.H., P.11576). Ventrally the postrostral joins the rostro-premaxillary and this latter bone forms the anterior



extremity of the upper jaw and bears four or five pointed teeth. The rostromaxillary can be seen on B.M.N.H., P.11577 where it has been displaced and lies in front of the skull. The antorbital bears a few teeth ventrally and the contained infraorbital sensory canal has the primitive "Y" shaped bifurcation. There are two members of the infraorbital series, a long ventral member which borders the lower margin of the orbit and a second considerably expanded bone which joins it posteriorly and forms part of the posterior rim of the orbit. This second infraorbital is much more plate-like, fitting neatly beneath the suborbitals. The sensory canal, as it passes through this infraorbital, gives off numerous finer branches posteriorly. Dorsally this infraorbital joins the dermosphenotic anteriorly and the second suborbital posteriorly. The dermosphenotic is a narrow but stout bone which dorsally fits under the lateral edge of the dermopterotic and extends anteriorly just to meet the nasal. Behind the dermosphenotic lies a pair of suborbitals. The orbit itself has an ossified sclerotic ring made up of four segments. The upper segment can be seen on R.S.M. 1896.34.1, where the centre is feebly ornamented with a few tubercles but the remainder is mainly smooth bone.

The maxilla is of the normal palaeoniscoid pattern and bears two series of teeth as in *Elonichthys* Giebel, a row of large pointed teeth interspersed with a series of much smaller teeth. The tooth series extends right up to the posterior extremity of the maxilla. The preopercular is a little higher than the maxilla, and the preopercular sensory canal passing along its length is distinctly elbowed about a third of the way up.

The opercular is approximately rhomboidal in outline with its antero-ventral margin cut away for the reception of the accessory opercular.

A conspicuous feature of the lateral wall of the skull is the presence of both "X" and "Y" bones, the upper of which is common in long-jawed palaeoniscoids. The terminology used in the past for these two bones is very confusing, but for the sake of completeness I will cite it. First the dorsal bone which lies in front of the opercular, between it and the dorsal edge of the preopercular. Traquair (1901 : 84) in describing *Watsonichthys pectinatus* (Traquair) referred to this bone as "X", but Watson (1925 : 819) in his description of *Cheirolepis trailli* Agassiz referred to the corresponding bone as "Y". Aldinger (1937 : 16) however called it a dorsal anteroperculum, but in recent times it has been given the name of dermohyal (Nielsen, 1936 : 42). Since there is in all probability a relationship between this dorsal bone and the underlying hyomandibular, I think the term dermohyal a convenient one and as such shall retain it.

Secondly, the ventral bone which lies between the antero-ventral corner of the opercular and the preopercular. Traquair (1877c : 47) first called this bone the suboperculum, then later referred to it as the interoperculum (1890 : 397). Later again Traquair (1901 : 62) considered it an "accessory plate", but in the same work (1901 : 84) in describing *Watsonichthys pectinatus* (Traquair) he calls it bone "Y". Watson (1925 : 819) in describing *Cheirolepis trailli* Agassiz referred to it as bone "X", while Aldinger (1937 : 16) considered it to be a ventral anteroperculum. Nielsen (1936 : 42) used the term ventral dermohyal for this bone, but Rayner

(1951 : 57) although doubting its relationship with the hyomandibular retains the term for the sake of convenience. Pehrson (1940) from a study of the development of the dermal bones of the skull of *Amia calva* believes that both the "X" and "Y" bones (of Watson, 1925 : 819) in *Cheirolepis trailli* came from primordia developed in relation to the preopercular canal. Stensiö (1947 : 149, 152) believes that both the dermohyal and bone "X" of Watson (1925 : 819) are anamestic components of the preopercular plate, corresponding to similar anamestic components of the preopercular plate in the Porolepiformes. Lehman (1947 : 17) follows Pehrson (1940) and Stensiö (1947) and has coined the term epipreopercular for the bone "X" of Watson (1925 : 819). Rayner (1951 : 57) however thinks that "the ventral dermohyal is simply an extra bone in the opercular series", and after studying other palaeoniscoids in which this bone occurs, *Watsonichthys*, *Cosmoptychius*, *Kentuckia* and *Rhabdolepis* I consider this to be the most sensible view and use the term accessory opercular when describing this bone.

The accessory opercular is triangular in outline with the ventral margin concave where it fits over the subopercular. Consequently the shape of the subopercular is altered for the reception of the accessory opercular, its dorsal margin not being straight as is the more normal condition, but convex. Between the opercular and the preopercular and above the accessory opercular lies the dermohyal. This bone is broadest dorsally and narrows almost to a point ventrally. From the angle of these opercular bones the suspensorium can be seen to be oblique. The subopercular is succeeded by approximately twenty branchiostegal rays and there is a median gular between the jaw rami.

*The Lower Jaw.* The greatest portion of the jaw is made up of the dentary. The surangular is relatively large and forms a neat socket for the articulating surface of the upper jaw. The remainder of the posterior edge is made up of the angular which is very stout near the jaw articulation. The upper margin of the jaw is straight, except posteriorly, where it extends upwards to give a high prominence to the back end of the jaw which bears the articulatory facet. The teeth are of two main sizes, the large ones which are smooth and with a well-defined enamel cap covering the last few mm. of tooth and which bear striations immediately below the cap, and the smaller tooth series which fills in the spaces between the larger teeth.

The palate has been adequately described by Watson (1925 : 851) and is very similar to that seen in *Namaichthys schroederi* Gürich (Gardiner, 1962).

Fragments of the hyobranchial apparatus can be seen in R.S.M. 1890.133.17, where several of the ceratobranchials of the left side are visible. These are long, smooth, and similar in size. The hyomandibular is stout and inclined, lying beneath the dermohyal and the posterior edge of the preopercular, and is similar in shape to that seen in *Pteronisculus* (Nielsen, 1942).

*The paired fins and their girdles.* The supracleithrum is large and extends down beyond the ventral limit of the opercular. The cleithrum is stout, distinctly curved and expanded ventrally and with large clavicles succeeding it anteriorly. The bones of the pectoral girdle are more or less longitudinally striated.

The pectoral fin has about fifteen to twenty rays, the first eight of which are the largest and are unjointed for the initial third of their length. The rays are delicately ornamented with a few oblique striae (R.S.M. 1890.104.11).

The pelvic fin is slightly smaller, with about twenty rays all jointed to their bases. The fin has a long base line, much longer than in *Elonichthys* Giebel, and in this respect it resembles both *Cheirolepis* Agassiz and *Cosmoptychius* Traquair. Both pectoral and pelvic fins bear numerous fulcra.

*The unpaired fins.* Both the dorsal and anal fins are large with stout rays. The dorsal fin has about thirty-five to forty rays which are strongly ornamented with longitudinal striae. There are four to six large ridge scales in front of the dorsal fin and the fulcral scales form a stout anterior border to the fin.

The anal fin has about thirty five rays and a distinct fringe posteriorly ; in this respect it resembles *Pygopterus* Agassiz. The ornamentation is slighter than on the dorsal fin and there is only one large ridge scale preceding it. The fulcral scales are again large and on some specimens the radials supporting the fin can be made out. The radials are long, the first radial articulating with about six lepidotrichia, its distal end being much widened. The remaining radials are only slightly thickened distally (R.S.M. 1892.138.5, B.M.N.H., P.11577).

The caudal fin is heterocercal, inequilateral and deeply cleft.

*The squamation.* The characteristic ornamentation and shape of the scales of this species have been well described and figured by Traquair. The scales are ornamented with ridges of enamel which run longitudinally along the length of the scale and terminate in nine or more serrations or teeth posteriorly and to which the specific name *W. pectinatus* (Traquair) refers. The ridges often branch once anteriorly and once posteriorly. The ridge scales of the axial lobe are ornamented on their free areas with small striated tubercles.

### Genus *COSMOPTYCHIUS* Traquair, 1877b

1835 *Amblypterus* Agassiz, *partim*, 2, 1, p. 111, pl. 4b, figs. 3-6.

1857 *Rhabdolepis* Troschel, *partim*, p. 16.

1890 *Elonichthys* Traquair, *partim*, pp. 390, 396.

DIAGNOSIS (emended). Body deeply fusiform ; dorsal fin arising well in front of anal, both fins large and triangular, the former being slightly larger ; caudal fin powerful, deeply cleft and inequilateral ; pectoral fin with rays articulated except just at commencement of first two rays at lateral margin of fin, and pelvics long based ; all fins with numerous small fulcra anteriorly and lepidotrichia distally bifurcated. Skull rounded anteriorly, without a well developed rostrum and with only one pair of extrascapulars, suspensorium very oblique and orbit large ; opercular long and narrow, much longer than subopercular with antero-dorsal dermohyal and antero-ventral accessory opercular. Preopercular very narrow and produced antero-dorsally to fit over the top of first suborbital, branchiostegal rays numerous, suborbitals present. Head bones sculptured with sharply defined, nearly parallel, branching and anastomosing ridges of enamel ; gape wide, teeth consisting

of closely set, rather small, conical lanianaries with outer series of much smaller teeth ; scales large, rhomboidal, with pronounced, oblique striae, flank scales higher than broad.

TYPE SPECIES. *Amblypterus striatus* Agassiz.

REMARKS. This genus was erected by Traquair (1877b : 553 ; 1877c : 43) to incorporate the single species described by Agassiz (1835 : 111) as *Amblypterus striatus*. Traquair (1890 : 390), however, decided that this species did not in fact belong to a new genus, as he had previously supposed, neither did it belong to the essentially Permian genus *Amblypterus* Agassiz (1835 : 111), but that it belonged to the genus *Elonichthys* Giebel, a view supported later by Woodward (1891 : 491), who lists *Cosmoptychius* Traquair as being synonymous with *Elonichthys*. Watson (1928 : 49), when describing the neurocranium of *striatus* Agassiz, refers the species to the genus *Cosmoptychius* Traquair. Finally, Aldinger (1937 : 312) pointed out that from the shape of the parasphenoid alone *striatus* Agassiz differed so much from the genus *Elonichthys* that it was necessary to retain the genus *Cosmoptychius* Traquair for its reception. He then linked *Cosmoptychius* with *Nematoptychius* Traquair and *Pygopterus* Agassiz in the new family Pygopteridae.

### *Cosmoptychius striatus* (Agassiz)

(Text-figs. 2, 3)

- 1835 *Amblypterus striatus* Agassiz, 2, 1, p. 111, pl. 4b, figs. 3-6.
- 1837 *Amblypterus striatus* Agassiz : Paterson, p. 153.
- 1854 *Amblypterus striatus* Agassiz : Morris, p. 317.
- 1857 *Rhabdolepis striatus* (Agassiz) Troschel, p. 16.
- 1877b *Cosmoptychius striatus* (Agassiz) Traquair, p. 553.
- 1877c *Cosmoptychius striatus* (Agassiz) : Traquair, p. 43, pl. 2, fig. 7, pl. 3, figs. 1-8.
- 1888 *Cosmoptychius striatus* (Agassiz) : Sauvage, p. 42, pl. 16, fig. 3.
- 1890 *Elonichthys striatus* (Agassiz) Traquair, pp. 390, 396.
- 1891 *Elonichthys striatus* (Agassiz) : Woodward, p. 491.
- 1901 *Elonichthys* (*Cosmoptychius*) *striatus* (Agassiz) : Traquair, p. 84, footnote 1.
- 1907 *Elonichthys striatus* (Agassiz) : Traquair, p. 107.
- 1928 *Cosmoptychius striatus* (Agassiz) : Watson, p. 49, text-figs. 1-3.
- 1937 *Cosmoptychius striatus* (Agassiz) : Aldinger, p. 312.
- 1954 *Elonichthys striatus* (Agassiz) : Waterston, p. 67.

DIAGNOSIS (emended). Fishes not exceeding 28 cm. in total length, body fusiform, length of head contained four times and greatest depth of body three times in total body length. Dorsal and anal fins similar in size, pelvic fin long based. Lepidotrichia of fins striated partly longitudinally and partly diagonally ; ornamentation of scales characteristic ; four ridge scales in front of dorsal, one in front of caudal fins, ridge scales of axial lobe commencing some way behind dorsal fin. See also Traquair 1877c : 43.

SYNTYPES. R.S.M. 1878.18.1, 1878.18.2 and 1878.18.3, all from the Calciferos Sandstone Series, Wardie, Edinburgh. I designate R.S.M. 1878.18.2 as the lectotype.



**MATERIAL.** Specimens including the syntypes from the Royal Scottish Museum and from the British Museum (Nat. Hist.). Fifteen specimens were examined, in five of which the skull was well preserved and in counterpart.

**DESCRIPTION.** *The skull.* The dermal bones of the skull and the sensory canal system, as far as can be determined, are shown in Text-fig. 2. The snout is rounded as in *Watsonichthys pectinatus* (Traquair) and not produced into a rostrum as in the genus *Elonichthys* Giebel.

The skull roofing bones are all ornamented with ridges of enamel which run parallel to one another and which occasionally branch and anastomose : nowhere do these ridges give way to tubercles. On the frontals, nasals and rostral these ridges follow the length of the bone, but on the dermopterotic the ridges follow a more sinuous course, starting at the posterior, inferior corner, they pass upwards, then curve gently downwards and then more gently upwards again, to reach the anterior edge of the bone, only occasionally branching and anastomosing. The ridges on the extrascapulars and suprascapulars run transversely from the mid-line of the skull out to the lateral edges. The ornamentation of the opercular series, maxilla, suborbitals, branchiostegal rays and lower jaw has already been figured by Traquair (1877c, pl. 3, fig. 3). On the opercular the ridges on the posterior half of the bone follow the outline of that bone, while on the anterior half they run up and across more or less diagonally. The ridges of ornament on the subopercular and branchiostegal rays run antero-posteriorly dividing and anastomosing. On the supracleithrum these ridges run diagonally across the length of the bone. However, on the maxilla the ridges of enamel follow the contour of the bone, passing upwards from the postero-ventral corner, across the top of the bone and then curving downwards when they reach the anterior edge ; several ridges run lengthways along the ventral edge. The majority of the ridges of enamel on the maxilla run parallel to one another along the whole of their length, as though engraved there by a precision tool. Over the anterior two-thirds of the preopercular the ridges pass from the mid-line of the bone, upwards to the dorsal edge, and downwards and backwards in a diagonal fashion to the ventral edge, giving the bone a herring-bone type of patterning. On the dermohyal the striae follow its long axis, whilst on the accessory opercular they run more obliquely. Of the suborbital series, the ornament on the dorsal member runs across horizontally while that of the ventral member runs across from the anterior edge, curves downwards and then follows the ventral edge of the bone. On the dermosphenotic the ridges in part follow the length of the bone (dorsally) and in part run horizontally across it (ventrally). Again on the second infraorbital the ridges run across almost horizontally. Ventrally on the lower jaw the ridges of ornament follow its entire length, but from the mid-line they run diagonally forwards and upwards to the dorsal jaw edge. In summing up this ornamentation I quote Traquair (1877c : 44) : " Nothing can exceed the beauty of the sculpture of the external surfaces of these facial bones, which consist of delicate yet sharply defined, nearly parallel, and slightly wavy, branching and anastomosing ridges ".

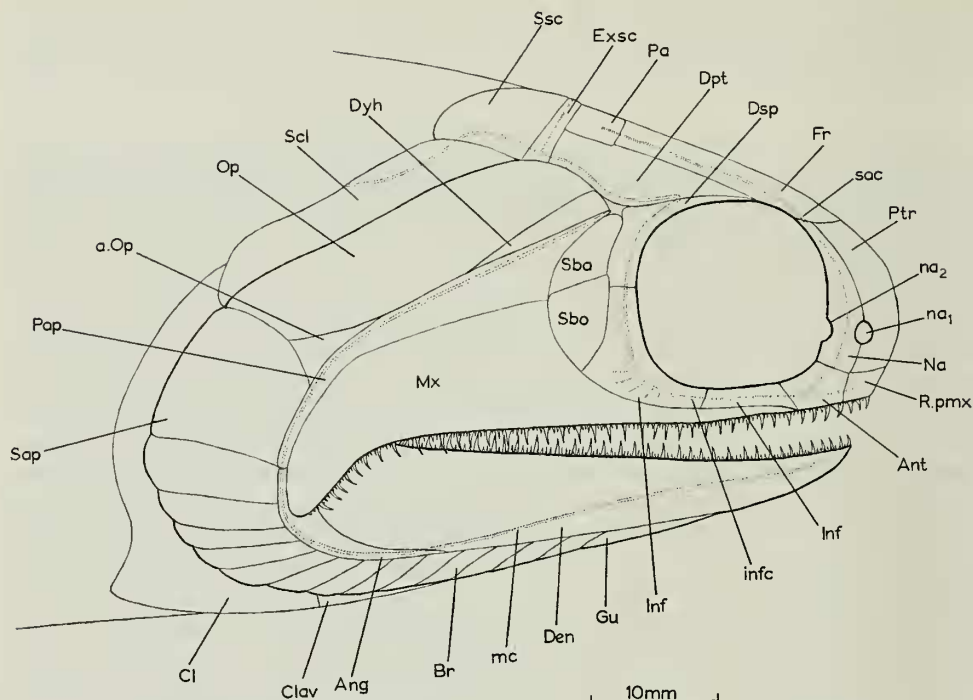


FIG. 2. *Cosmoptychius striatus* (Agassiz). Reconstruction of skull in lateral view.

The skull is characterized by its oblique suspensorium and the make up of the opercular apparatus. The suprascapulars are stout, bluntly rounded posteriorly and joined to a single pair of narrow extrascapulars. The parietals are small and square and the greater portion of the skull roof is made up by the large rectangular frontals. The dermopterotics are small and do not extend far enough to meet the nasals anteriorly. The postrostral is a stout ossification whilst the nasals are thinner and more delicate. Ventrally the nasals join the toothed antorbital and there is some evidence of a rostromaxillary bone in front of the antorbital and beneath the postrostral. The snout is bluntly rounded (R.S.M. 1859.33.71 and counterpart). There are but two members of the infraorbital series. The first is short and rectangular joining the antorbital anteriorly and the maxilla ventrally. The second infraorbital has an expanded basal portion which is concave posteriorly where it fits under the suborbital series. Dorsally the second infraorbital meets the dermosphenotic. The dermosphenotic forms the upper posterior margin to the orbit and extends forwardly just to meet the frontal. The suborbital series consists of two bones, the lower of which is the larger; both are approximately triangular in outline (R.S.M. 1859.33.71). Occasionally these two bones are fused into a single ossification (R.S.M. 1875.29.153). The maxilla is of the normal palaeoniscoid pattern and curves slightly upwards before it meets the antorbital. The ventral

margin bears teeth along its entire length, the teeth being in two series ; a series of stout, sharp, incurved, conical teeth which are closely set, and an outer series of much smaller teeth. The preopercular is a very narrow bone, as narrow as that seen in the genus *Cycloptychius* Young. Anteriorly it is produced almost to a point where it fits over the upper of the two suborbitals. Dorsally the preopercular does not extend far enough to meet the dermopterotic. Above the preopercular is a wedge-shaped dermohyal tapering to a point ventrally. Dorsally it abuts on to the dermopterotic. The opercular is also a narrow bone, with both the antero-dorsal and antero-ventral corners bevelled to admit the dermohyal and the accessory opercular respectively. Similarly the antero-dorsal corner of the subopercular is bevelled to make room for the accessory opercular. Apart from this, however, the subopercular is nearly square, but rather broader posteriorly. The branchiostegal rays number approximately fifteen, with a lozenge-shaped gular plate anteriorly.

*The lower jaw.* The mandible is stout with an upper margin which curves slightly upwards at its extremity. The greater portion of the outer surface of the jaw is made up by the dentary. The angular, which is a stout ossification, makes up the posterior border. The posterior end of Meckel's cartilage is completely ossified, forming a stout articular. The upper border of the dentary supports a series of large, curved teeth, which posteriorly are directed forwards. These laniary teeth are closely set, the distance between them being less than their own length, and by comparison with *Watsonichthys pectinatus* (Traquair) they are relatively small teeth. Outside these laniary teeth is a series of much smaller teeth, less than half the size of the inner series. The shelf on which these laniary teeth are set is overlapped at its inner edge by the coronoid bone.

*Palate.* The palatoquadrate cartilage is completely ossified and the most extensive bone is the entopterygoid (pterygoid of Watson, 1925). The entopterygoid is distinctly concave and of pronounced semi-cylindrical shape. Posteriorly it joins the smaller ectopterygoid. The ectopterygoid bears a series of pointed teeth continuous with those on the palatine, the palatine being attached to the anterior end of the ectopterygoid. Posteriorly the ectopterygoid is fused to the stout quadrate. Above the ectopterygoid is an expanded, more lightly ossified metapterygoid, and the suprapterygoid series forms an anterior extension to the metapterygoid and also the hinder margin to the deep notch through which the maxillary and mandibular branches of the fifth nerve passed. The general make up of the palatoquadrate apparatus then is not very different from that described for *Nematoptychius greenocki* (Traquair) by Watson (1928, text-fig. 7).

The hyomandibular, the only other visible component of the visceral arch skeleton, is much more distinctly elbowed than in *Pteronisculus* White. It can be clearly seen in specimen R.S.M. 1926.57.22, and is blade-shaped dorsally with a stout axial ridge. Ventrally the bone is elbowed and the lower shaft is circular in cross section. The hyomandibular lies immediately beneath the preopercular and is similar in shape.

*The Neurocranium.* This has been adequately described by Watson (1928 : 49, text-figs. 1-4).

*The paired fins and their girdles.* The primary girdle is ossified, both the scapulocoracoid and mesocoracoid regions being apparent. Specimen R.S.M. 1857.33.71 shows clearly four radial elements (Text-fig. 3). The second radial from the lateral edge of the fin is hour-glass shaped, whilst the two innermost members are stout and almost straight rods. Distally the first two radials (numbering from the lateral edge) articulate with four smaller ossifications; these probably represent the ossified distal cartilages of the radials. The third radial articulates directly with six lepidotrichia and the fourth probably with three lepidotrichia. The lepidotrichia number about nineteen, and they are jointed throughout their length except at the bases of the first two rays of the lateral margin. The lepidotrichia are delicately ornamented with two distinct ridges anteriorly, which run along the length of the ray, and posteriorly with short diagonal ridges of enamel that run from about the mid-line out and away from the fin base, to the posterior edge of the ray.

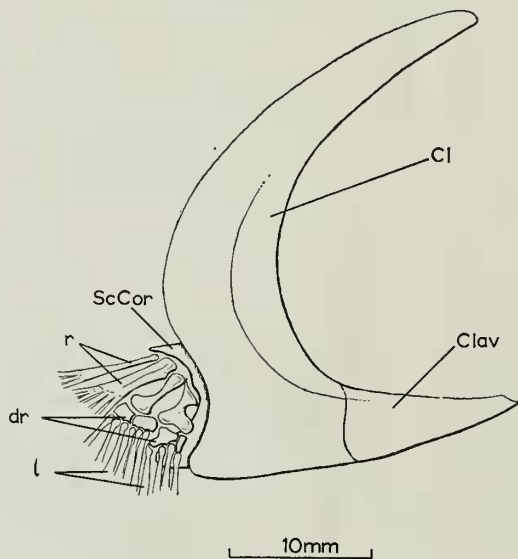


FIG. 3. *Cosmoptychius striatus* (Agassiz). Reconstruction of pectoral girdle. Mainly from R.S.M. 1857.33.71.

The pelvic fin is very long based with about forty to forty-five fin rays, and similar ornamentation to the pectorals, except that instead of two ridges of enamel running lengthways along the rays anteriorly there is only one. Both pectoral and pelvic fins bear fulcral scales.

*The unpaired fins.* Both dorsal and anal fins are triangular, the dorsal being somewhat the larger. Both have about forty lepidotrichia and are fringed anteriorly by pointed fulcral scales. The ornamentation of these two fins is essentially similar to that on the pectoral as far as the anterior fin rays are concerned, but on the more



posterior rays there is only one longitudinal ridge (Traquair, 1877, pl. 13, fig. 3). The caudal fin is heterocercal, deeply cleft and inequilateral.

*The squamation.* The scales from the middle of the flank are nearly twice as deep as broad. The scale ornamentation consists of fine, sharply defined, parallel ridges of enamel which pass diagonally downwards and backwards across the scale. These ridges sometimes branch, and occasionally anastomose. The ridges extend beyond the posterior scale margin to give it a delicately serrated appearance (i.e. the margin is delicately denticulated). Woodward's (1891 : 491) statement that none of the scales is posteriorly serrated is thus erroneous.

### Family ACROLEPIDAE

DIAGNOSIS. See Aldinger, 1937 : 32, 250.

REMARKS. The genus *Mesonichthys* gen. nov. clearly belongs to Group A of the family Acrolepidae (Aldinger, 1937 : 250) and bears many resemblances to *Acrolepis sedgwicki* Agassiz, in particular the abnormally high position of the external nares (see Westoll in Aldinger, 1937, text-fig. 74).

### Genus *MESONICHTHYS* nov.

1886 *Elonichthys* Traquair, *partim*, p. 440.

1937 *Watsonichthys* Aldinger, *partim*, p. 256.

DIAGNOSIS. Body fusiform ; dorsal fin arising well in front of anal, both fins triangular, acuminate and similar in size ; caudal fin deeply cleft and inequilateral ; pectoral fin long, with principal rays unjointed in proximal third of their length, pelvics short based ; all fins have numerous fulcra anteriorly and lepidotrichia distally bifurcated. Snout rounded anteriorly and not produced into a rostrum. Jaw suspension only moderately oblique and opercular more than twice as high as subopercular. Orbit large with well developed sclerotic ring ; dermohyal present but no accessory opercular ; suborbitals present ; angle of preopercular approximately 60° ; cranial roof bones and cheek bones ornamented with ridges of enamel ; teeth of two sizes, larger conical caninaries being closely set with smaller tooth series interspersed ; scales rhomboidal with pronounced ridges.

TYPE SPECIES. *Elonichthys aitkeni* Traquair.

REMARKS. *Mesonichthys aitkeni* (Traquair) was placed in the genus *Elonichthys* Giebel by Traquair (1886 : 440). Aldinger (1937 : 256) concluded that this species was not a member of the genus *Elonichthys* because the principal lepidotrichia of the pectoral fins were unjointed and suggested its inclusion in the genus *Watsonichthys*. He also pointed out (p. 207) that the form of the opercular, the scale ornamentation and the shape of the metapterygoid suggested it was an acrolepid. However, the genus *Watsonichthys* is characterized by, amongst many other features, the presence of an accessory opercular. No accessory opercular occurs in *Mesonichthys aitkeni* (Traquair), and it is necessary to erect a new genus for the reception of this species.

***Mesonichthys aitkeni*** (Traquair)  
(Text-fig. 4)

- 1874 *Acrolepis* sp. Aitken, p. 36.  
 1886 *Elonichthys aitkeni* Traquair, p. 440.  
 1890 *Elonichthys aitkeni* Traquair : Ward, p. 174, pl. 6, figs. 9, 12.  
 1891 *Elonichthys aitkeni* Traquair : Woodward, p. 490.  
 1895 *Elonichthys aitkeni* Traquair : Bolton, pl. 3, fig. 14.  
 1898 *Elonichthys aitkeni* Traquair : Welburn, p. 426, pl. 62, fig. 5.  
 1901 *Elonichthys aitkeni* Traquair : Traquair, pp. 77-80, pls. 16, 17, figs. 1-7.  
 1907 *Elonichthys aitkeni* Traquair : Rogers, p. 394.  
 1919 *Elonichthys aitkeni* Traquair : Pruvost, p. 404, pl. 28, fig. 11.  
 1925 *Elonichthys aitkeni* Traquair : Watson, p. 855, text-fig. 23, p. 862, text-fig. 29.  
 1930 *Elonichthys aitkeni* Traquair : Pruvost, p. 124.  
 1932 *Elonichthys aitkeni* Traquair : Susta, p. 136, pl. 1, figs. 16, 17.  
 1934 *Elonichthys aitkeni* Traquair : Keller, p. 50, pl. 5, fig. 10.  
 1937 *Elonichthys aitkeni* Traquair : Aldinger, p. 207.  
 1937 *Watsonichthys* (?) *aitkeni* (Traquair) Aldinger, p. 256.  
 1939 *Elonichthys aitkeni* Traquair : White, p. 42.  
 1941 *Elonichthys aitkeni* Traquair : Demanet, p. 174, pl. 11, figs. 3-10.  
 1943 *Elonichthys aitkeni* Traquair : Heide, p. 29, fig. 2.  
 1945 *Elonichthys aitkeni* Traquair : Dorsman, p. 78, pl. 11, fig. 3.  
 1955 *Elonichthys aitkeni* Traquair : Heide, p. 74, pl. 17, fig. 32.

DIAGNOSIS (emended). Fishes not exceeding 18 cm. in total length, body fusiform, length of head contained five times and greatest depth of body four times in total body length. Lepidotrichia slender and smooth. Scales of moderate size, deeper than broad on the flank and ornamented with prominent striae which run obliquely across the scale. Striae straight, rarely bifurcated or interpolated, and run parallel to one another. See also Traquair, 1901 : 77.

LECTOTYPE. From Traquair's original description (1886 : 440) of the species only one specimen is identifiable. This specimen was figured in a later paper by Traquair (1901, pl. 16, fig. 1) and was an imperfect fish from the collection of J. Aitken. It came from the "Copy" Coal Mine, Cliviger, Lancashire. Woodward (1891 : 490) nominated this same specimen as the type. Unfortunately, even when figured by Traquair in 1901, this specimen had already been lost. Since it seems very unlikely that this lectotype of Woodward's will ever be found, I nominate as the neotype B.M.N.H., P.6100 from the Culm-Measures, Instow, North Devon, figured by Traquair (1901, pl. 17, fig. 7).

MATERIAL. Specimens, including the neotype, from the British Museum (Nat. Hist.) and the Geological Survey Museum. Ten specimens were examined.

REMARKS. One specimen in the Geological Survey Museum, No. 4520 and counterpart, figured by Traquair (1901, pl. 16, fig. 2) was probably one of the specimens on which he based his original description (1886 : 440).

DESCRIPTION. *The skull.* The shape of the skull is given in Text-fig. 4. The snout is rounded as in *Watsonichthys pectinatus* (Traquair). The external skull bones are all very strongly ornamented with ridges of enamel. On the frontals,

parietals, dermopterotics and suprascapulars these ridges of enamel follow the length of the bone. Many of the ridges run the whole length of these bones and a small percentage of them occasionally branch, but not usually more than once. On the postrostral the ridges of enamel are shorter and break up into tubercles anteriorly, while on the nasals the ridges are longer and follow the long axis of the bone. The ridges of enamel on the dermosphenotic and the two suborbital bones, however, run across the bones from front to back, a few of the ridges branching, more particularly on the suborbitals. Again, on the more posterior infraorbital the ridges run horizontally on its dorsal region, but ventrally the ridges become more vertical in their course. The ornamentation on the antorbital and rostrum-premaxillary consists of shorter ridges running parallel to the long axis of the fish. Along the ventral edge of the maxilla the ridges of enamel are also short and follow the bone margin. On the greater portion of the maxilla the ridges are long and pass upwards and forwards to the dorsal margin, occasionally branching. On the dorsal extremity of the preopercular the ridges run across the bone from front to back, but more ventrally the ridges branch, become much more sinuous and sweep slightly upwards. The ornamentation on the dermohyal consists of well marked ridges which run more or less parallel to the short axis of this bone. On the opercular some of the ridges are very long and pass diagonally from the posterior ventral corner to the dorsal anterior corner, and the rest of the ridges run more or less parallel to these. The ridges which ornament the preopercular make a far different pattern from that seen on any of the other skull bones. The ridges sweep upwards from the posterior ventral corner towards the dorsal margin, curve downwards until they almost reach the middle point of the anterior margin and then curve back on themselves and follow a sinuous course back to the ventral edge. The effect of this is to give a roughly oval-shaped central area to the preopercular. The ornamentation of the mandible is somewhat variable but basically the ridges of enamel follow the length of the bone ventrally, while for the major portion of the mandible the ridges sweep upwards and forwards to the dorsal margin of the jaw. On the branchiostegal rays and gular plate the ridges follow the long axis of the bones and branch occasionally, usually not more than once. The pectoral girdle is well ornamented and on the cleithrum, supracleithrum and clavicles the ridges tend to follow the contours of the bones and occasionally bifurcate. The sclerotic ring is also ornamented but only with very feeble striae.

The skull of *Mesonichthys* is compact as in *Acrolepis* and not drawn out anteriorly as in *Elonichthys*. The orbit is situated well forward and the suspensorium is only moderately oblique. The suprascapulars are not as large as those in *Watsonichthys* and are joined to a single pair of narrow extrascapulars. The small, square parietals are preceded by a large pair of rectangular frontals. The dermopterotic is almost triangular in outline and extends laterally beyond the upper margin of the dermohyal nearly to meet the dorsal-most suborbital. Anteriorly the dermopterotic tapers to a point where it meets the nasal. The frontals join the postrostral and the nasals anteriorly. The postrostral is a large ossification, V-shaped where it fits between the two frontals (B.M.N.H., P.600). The nasal tapers sharply dorsally, joins the

antero-lateral edge of the frontal for a short distance and fits neatly over the anterior extremities of the dermopterotic and the dermosphenotic. Both the postrostral and the nasals curve downwards anteriorly, to give the snout a rounded shape (B.M.N.H., P.6100). Ventrally the postrostral joins the rostro-premaxillary. Both the rostro-premaxillary and the antorbital, which meets the rostro-premaxillary posteriorly, bear pointed teeth (B.M.N.H., P.36246).

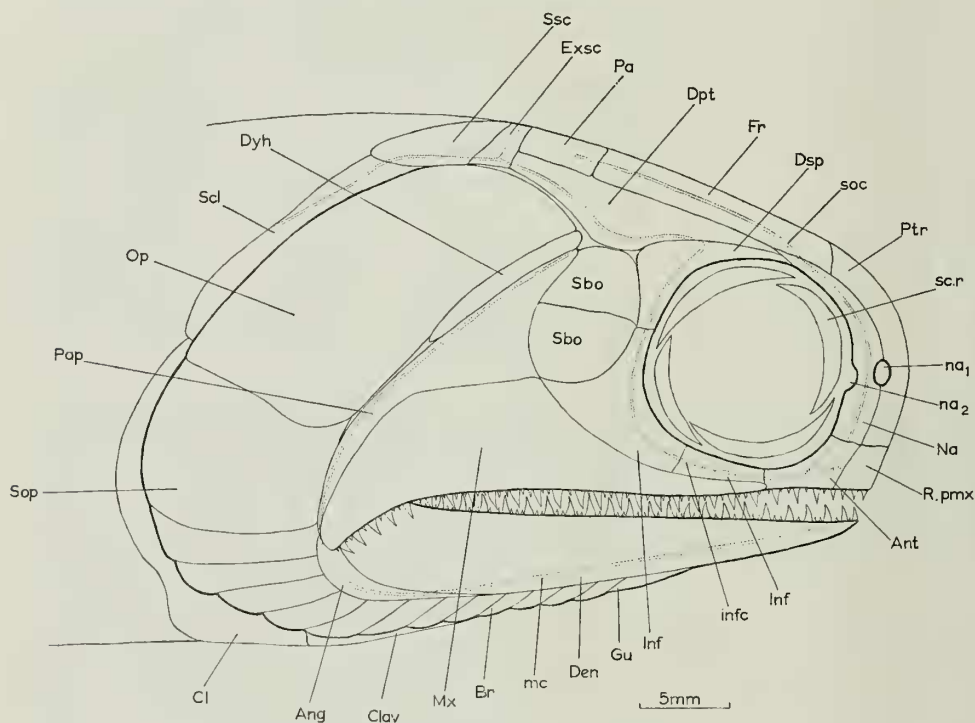


FIG. 4. *Mesonichthys aitheni* (Traquair). Reconstruction of the dermal bones of the skull in lateral view.

There are only two members of the infraorbital series. The first is a short rectangular bone which joins the antorbital anteriorly and the maxilla ventrally. Posteriorly it is united with the second infraorbital. The second infraorbital forms half of the posterior margin of the orbit and is concave anteriorly. This infraorbital is also concave posteriorly where it fits under the second suborbital bone, whilst ventrally its margin is convex. Dorsally the second infraorbital joins the dermosphenotic. The dermosphenotic forms the upper posterior quarter of the orbit's margin, and posteriorly it is concave where it fits round the first suborbital.

The suborbital series consists of two bones of approximately the same size and which together are oval in outline. The lower suborbital is rounded ventrally while the upper is rounded dorsally, the suture between them is straight.



The orbit has a sclerotic ring made up of four segments of which the two dorsal members are the largest.

The maxilla is of normal palaeoniscoid shape except that the anterior ventral margin turns slightly upwards before it meets the antorbital. The ventral margin bears teeth along the whole of its length. The teeth are of two sizes, a series of large conical teeth interspersed with a series of smaller teeth. The preopercular is a high bone with its posterior margin much nearer the vertical than that of *Elonichthys* or *Watsonichthys*. Anteriorly the margin of the preopercular is distinctly concave for the reception of the two suborbitals. Dorsally the preopercular does not meet the dermopterotic. Behind the preopercular lies a narrow dermohyal. The dermohyal tapers ventrally almost to a point, but dorsally it is rounded and extends a short distance beyond the dorsal limit of the preopercular.

The opercular is rectangular in outline with its dorsal margin gently rounded. The opercular is more than twice as high as the subopercular and more nearly vertical than the opercular in *Watsonichthys*. The preopercular is succeeded by twelve to fifteen branchiostegal rays and there is a median angular between the jaw rami.

*The lower jaw.* The greater portion of the lower jaw consists of dentary with the angular bone making up the posterior margin. The angular, when viewed from the outer jaw surface, does not extend very far along the ventral margin. The upper margin of the jaw is straight and bears teeth of two sizes. There is a series of large conical teeth, set much closer together than in the genus *Elonichthys* and a smaller tooth series which fills in the spaces between these larger teeth.

*The Palate.* The palate, hyobranchial apparatus and part of the neurocranium have been adequately described by Watson (1925 : 855, 862, figs. 23, 29).

*The Paired fins and their girdles.* The supracleithrum does not extend beyond the ventral limit of the opercular. The cleithrum is a stout ossification and is succeeded by an equally stout clavicle.

The pectoral fin is composed of between twenty and twenty-two rays, the principal members of which are unjointed for the initial third of their length. The rays are smooth and the anterior edge of the fin bears a row of fulcral scales. These fulcral scales form a pronounced fringe.

The pelvic fin is smaller with about fifteen rays, all jointed to their bases. The fin is relatively small, short based, and unornamented. Anteriorly there are numerous small fulcra.

*The Unpaired fins.* Both dorsal and anal fins are triangular, similar in size and with thirty-eight to forty-two rays. The fulcral scales are long and the fin rays are smooth, apart from a single longitudinal furrow just before they bifurcate. The caudal fin is heterocercal, inequilobate and deeply cleft.

*The squamation.* The scales have been adequately described and figured by Traquair. One peculiar ornamental character noted by Traquair is that the lowermost ridge on most of the body scales is united to the ridge above it, resulting in a broad, ventral ridge.

There is one large ridge scale in front of the anal fin, and several preceding the dorsal fin. The ridge scales of the axial lobe arise some distance behind the dorsal fin.

Family **PYGOPTERIDAE**

DIAGNOSIS. See Aldinger, 1937 : 309.

Genus **NEMATOPTYCHIUS** Traquair, 1875

1844 *Pygopterus* Agassiz, 2, 2, p. 78 (undefined).

1867 *Pygopterus* Traquair, *partim*, p. 701, pl. 45.

DIAGNOSIS (emended). Body elongate : dorsal fin situated far back nearly opposite anal, both triangular and of moderate size : caudal fin heterocercal and deeply cleft : paired fins moderate in size, pectoral fin with principal rays unarticulated for a short distance from origin, remainder of fin with closely articulated rays : all fins with distinct but small fulcra anteriorly and lepidotrichia distally bifurcated. Skull with distinct rostrum, very oblique suspensorium and relatively small orbit with stout sclerotic ring. Opercular long and narrow dorsally and no antero-dorsal dermohyal or antero-ventral accessory opercular. Rostro-premaxillary present and also suborbital series, branchiostegal rays numerous : head bones ornamented with ridges and tubercles, gape wide, dentition consisting of inner series of large, stout, conical laniaries, few in number, and outer series of more numerous smaller teeth ; scales small, only slightly imbricating, those of the flank much higher than broad with relatively large peg-and-socket articulation. Scale ornament consisting of delicate ridges of enamel.

TYPE SPECIES. *Nematoptychius greenocki* (Traquair).

REMARKS. This genus was erected by Traquair (1875 : 258) to incorporate the single species previously described by him (1866 : 597) as *Pygopterus greenockii*. The same author (1876 : 262) described a second species, *Nematoptychius gracilis*, but decided later (1890 : 391) that this was synonymous with *Nematoptychius greenocki* (Traquair). One of the specimens (R.S.M. 1875.29.127) which Peach (1872 : 109) used to erect the species *Pygopterus elegans* (nomen nudum) is also synonymous with *Nematoptychius greenocki* (Traquair).

***Nematoptychius greenocki*** (Traquair)

(Text-figs. 5-8)

1844 *Pygopterus greenockii* Agassiz, 2, 2, p. 78 (undefined).

1866 *Pygopterus greenockii* Traquair, p. 597.

1867 *Pygopterus greenockii* Traquair : Traquair, p. 701, pl. 45, figs. 1-4.

1872 *Pygopterus elegans* Peach, p. 109 (nomen nudum).

1875 *Nematoptychius greenockii* (Traquair) Traquair, p. 258, pl. 16, figs. 7-11.

1876 *Nematoptychius gracilis* Traquair, p. 262.

1877b *Nematoptychius greenockii* (Traquair) : Traquair, p. 577.

1877c *Nematoptychius greenockii* (Traquair) : Traquair, pp. 14, 15, pl. 1, figs. 7-11.

1879 *Nematoptychius greenockii* (Traquair) : Traquair, pp. 118, 128.

1890 *Nematoptychius greenockii* (Traquair) : Traquair, pp. 391, 398.

1891 *Nematoptychius greenocki* (Traquair) : Woodward, p. 458.

1907 *Nematoptychius greenocki* (Traquair) : Traquair, p. 111.

1909 *Nematoptychius greenocki* (Traquair) : Traquair, p. 116, pl. 26.

1925 *Nematoptychius greenocki* (Traquair) : Watson, p. 858, text-fig. 26.

1928 *Nematoptychius greenocki* (Traquair) : Watson, pp. 55, 59, text-figs. 7, 11.

1954 *Nematoptychius greenocki* (Traquair) : Waterston, p. 59.

1954 *Nematoptychius gracilis* Traquair : Waterston, p. 61.

DIAGNOSIS (emended). Fishes not exceeding 48 cm. in total length, body elongated, length of head contained almost five times and greatest depth of body more than five times in total body length. Dorsal and anal fins similar in size and opposed to one another, pelvic fin moderately long based. Lepidotrichia of fins closely articulated and not noticeably ornamented ; ornamentation of scales characteristic. See also Traquair, 1909 : 117.

SYNTYPES. R.S.M. 1926.57.44 and 1950.38.87, from the Calciferos Sandstone Series, Wardie, Edinburgh. Lectotype, R.S.M. 1926.57.44 as designated by Waterston (1954 : 59) and by Woodward (1891 : 458).

MATERIAL. Specimens, including one of the syntypes from the Royal Scottish Museum and from the British Museum (Nat. Hist.). Twenty-four specimens were studied including three showing the skull roofing bones and a fourth in which the head was uncrushed and preserved in the round.

REMARKS. *Nematoptychius greenocki* is widely distributed throughout the Lower Carboniferous rocks of eastern Scotland occurring from the Wardie Shales right up into the Upper Limestone Series. Traquair (1909 : 120) commenting on the predacious habits of some of the larger palaeoniscoids notes that in the abdominal cavity of one specimen of *N. greenocki* are the remains of a good-sized *Acanthodes*.

DESCRIPTION. *The skull.* The bones of the skull and course of the sensory canals are shown in Text-fig. 5. The most distinctive features are the pronounced rostrum and the absence of both dermohyal and accessory opercular bones.

The skull roofing bones are all ornamented with ridges of enamel, which in places give way to tubercles. On the parietals, frontals, dermopterotics and postrostral bones the ridges of enamel run more or less longitudinally along the length of these bones, the ridges are relatively short, dividing and anastomosing, and in places giving way to tubercles. The ridges of enamel on the extrascapular run across the bones, so that they are more or less continuous with those on the parietals and dermopterotics, whilst the suprascapular has very few ridges and is mainly tuberculated. The rostro-premaxillary also has an ornamentation of tubercles, but the nasals and the sclerotic ring are smooth. The maxilla has two distinct ornamentations, the oral margin is covered by large tubercles of enamel, while the remainder of the bone is covered by ridges, which sweep up and round the bone, running parallel with its posterior and superior borders. The infraorbitals and antorbitals are again tuberculated and the dermosphenotic has both tubercles and short ridges of enamel. On the suborbitals ridges of enamel run more or less dorso-ventrally. On the preopercular the ornamentation consists of short striae, and on the opercular the ridges follow the outline of that bone, running from top to bottom. The subopercular has fewer ridges, but more tubercles while the branchiostegal rays have mainly ridges which divide and anastomose and run more or less diagonally across the bones. The mandible is covered by short ridges and tubercles along its entire length ; the tubercles are more numerous anteriorly.

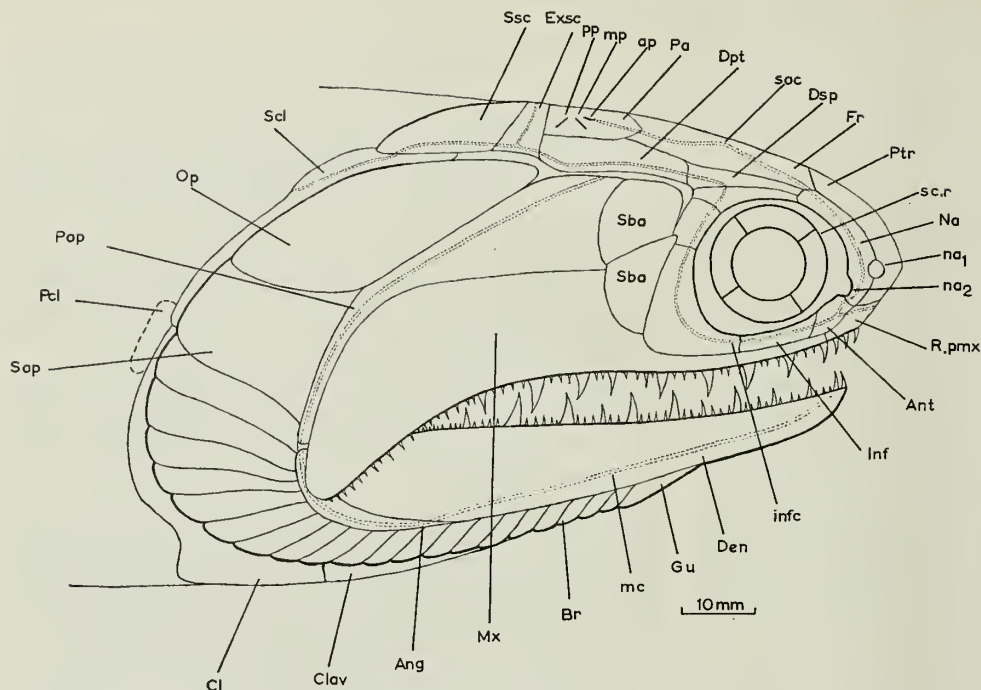


FIG. 5. *Nematoptychius greenocki* (Traquair). Reconstruction of skull in lateral view.

The skull of *N. greenocki* is long with an oblique suspensorium and the orbit situated well forward. The suprascapulars just meet in the mid-line anteriorly as do the single pair of extrascapular bones which precede them. The remainder of the skull roofing bones are known with much more certainty in this species than in most other palaeoniscoids of comparable age, since there are several specimens in which the cranial buckler has been preserved uncrushed, and some in which the whole head has been preserved in the round (R.S.M. 1892.137.6, 1891.111.9, 1950.38.87).

The paired parietals are rectangular with their anterior margins produced into a point (Text-fig. 6) and the sutures between them and the frontals anteriorly and the dermopterotics laterally are strongly digitated. The frontals are long and all the sutures between them and the other skull roofing bones equally toothed and digitate. Laterally the frontal is bordered by the dermopterotic, dermosphenotic and the nasal, whilst anteriorly the postrostral has a V-shaped insertion between the two frontals.

The lateral wall of the skull roof is comprised of three bones, the dermopterotic, the dermosphenotic and the infraorbital-supraorbital. The dermopterotic is the largest of these three bones and anteriorly joins the dermosphenotic. The dermo-



sphenotic passes forward to meet the nasal. The infraorbito-supraorbital lies alongside the dermosphenotic and overlaps it to a slight degree. Anteriorly the infraorbito-supraorbital also joins the nasal. The postrostral is only slightly curved from side to side in its posterior half, giving but a slight convexity to the dorsal surface; however, the anterior half of the bone is strongly curved in a transverse as well as a longitudinal direction, giving the head the typical palaeonisciform profile, that is a distinct rostrum. The radiation centre of the bone lies in its most arched part, in other words that region which forms the anterior tip of the rostrum.

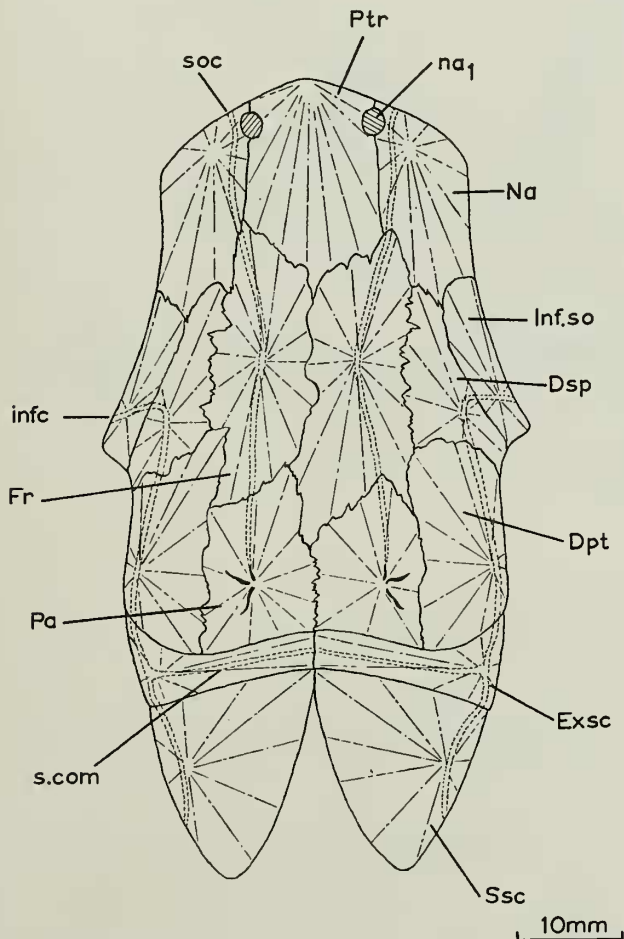


FIG. 6. *Nematoptychius greenocki* (Traquair). Dorsal view of skull roofing bones. From R.S.M. 1892.157.6, 1891.111.9 and 1890.78.4.

The nasal is stout and broad and its lateral margin forms together with the dorsal margin of the antorbital a distinct emargination ( $na_2$ ) which indicates the position

of the posterior nostril. The anterior nostril ( $na_1$ ) lies between the nasal and the postrostral. Posteriorly the nasal joins the frontal, dermosphenotic and the infraorbito-supraorbital. Anteriorly the postrostral meets the paired, toothed rostro-premaxillaries. The rostro-premaxillary can be distinguished on several specimens (B.M.N.H., P.11569, R.S.M. 1889.5.1) but its relationship to the neighbouring bones can best be seen on specimen R.S.M. 1950.38.87 from which Text-fig. 7 has been reconstructed. Most of the snout region in this specimen consists of an internal cast of the bones, and this shows the articulations of the individual bones more clearly. The rostro-premaxillaries overlap the anterior end of the postrostral, and running across the back of the rostro-premaxillaries in a transverse direction is a distinct groove (eth. com.). This groove in the rostro-premaxillaries carried the ethmoidal commissure. That this deduction as to the course of the ethmoidal commissure is correct and that Nielsen's (1942 : 136, fig. 32) view that the ethmoidal commissure ran along the back of the postrostral in *Pteronisculus gunnari* (Nielsen) is wrong is borne out by the course of the infraorbital sensory canal through the antorbital. The antorbital has the characteristic fork of the infraorbital canal in it, and also bears a rostral process through which the infraorbital canal passes (Text-fig. 7). This process fits behind the rostro-premaxillary, and is so positioned that the contained infraorbital canal is continuous with the groove (ethc.) in the back of the rostro-premaxillaries. The groove in the back of the postrostral in *Rhadinichthys fusiformis* Traquair has been correctly interpreted by Moy-Thomas & Dyne (1938 : 455, text-fig. 17) to be for the articulation of the front end of the palate and not a sensory canal groove, whilst a similar groove in the postrostral of *Pteronisculus gunnari* (Nielsen) is for the same purpose and not for the path of the ethmoidal commissure as it was interpreted by Nielsen (1942 : 136). The ethmoidal commissure, as far as can be judged, is never associated with the postrostral (see discussion).

The antorbital articulates with the nasal and rostro-premaxillary anteriorly and with the maxilla ventrally. Posteriorly the antorbital joins the first member of the infraorbital series. There are three infraorbitals of which the second is by far the largest (Text-fig. 5). The third infraorbital is short and dorsally joins the lateral corner of the infraorbito-supraorbital. Behind the infraorbital series are two suborbitals. Both suborbitals are strongly convex posteriorly where they fit into the anterior edges of the preopercular and maxillary bones. The ventral suborbital is roughly triangular in outline. The maxilla is of the normal palaeoniscoid outline, but not very high and curving upwards quite markedly towards its anterior extremity. The ventral margin of the maxilla bears teeth along its entire length ; the teeth are in two series, a series of stout, large, conical, slightly incurved teeth with smooth enamel caps and an outer series of smaller teeth. The preopercular is again of the normal palaeoniscoid form, but the preopercular sensory canal ends on the dorsal margin behind the anterior extremity of the bone.

The suspensorium is oblique and the opercular is not very large in comparison to the skull size. There are no accessory bones and the subopercular is less than half as high as the opercular. The preceding branchiostegal rays number approxi-

mately twenty and there is a small median gular plate. The orbit contains a large, smooth sclerotic ring which is probably composed of four segments (R.S.M. 1890.78.4 and an unregistered specimen from Straiton Oil Works).

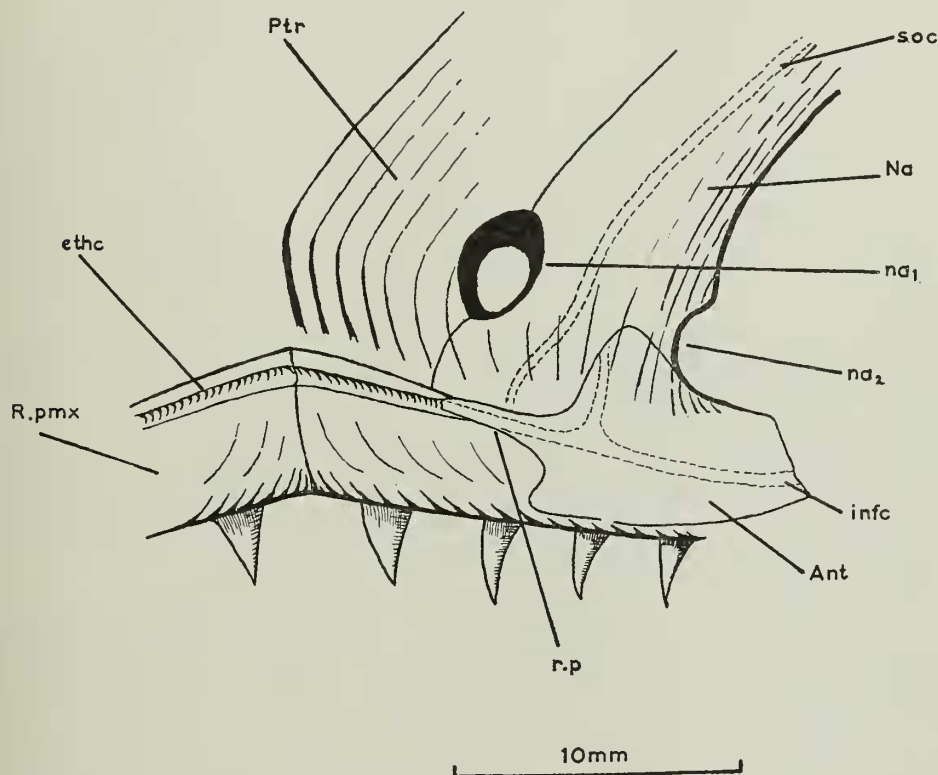


FIG. 7. *Nematoptychius greenocki* (Traquair). Snout region. From R.S.M. 1890.78.4.

*Lower jaw.* This has been adequately described by Watson (1925, text-fig. 11).

*Palate.* This has likewise been well described by Watson (1925, text-fig. 26 ; 1928, text-fig. 7).

*The paired fins and their girdles.* Of the pectoral girdle, the supracleithrum and cleithrum are ornamented with delicate tubercles and ridges of enamel. There is a pair of stout clavicles and posterior to the supracleithrum there appears to be a single member of the postcleithral series. There are ossified radials present, probably four in number ; these are hour-glass shaped and increase in length from the lateral towards the medial edge of the fin. The lepidotrichia of the pectoral fin number some fifteen members and the principal rays are unarticulated for a slight distance from their origin.

The pelvic fin has an extended base line and is composed of thirty or more rays.

*The unpaired fins.* The dorsal and anal fins are large and situated far back,

opposite one another, the anal being slightly the larger. The dorsal fin is formed of about forty rays and the anal forty-five. Both fins are triangular with closely articulated rays. The caudal fin is heterocercal, deeply cleft and inequilobate.

In several specimens some of the ossifications of the axial skeleton and the unpaired fins could be investigated in fair detail (R.S.M. 1950.38.87, 1889.5.1, etc.) (Text-fig. 8). The endoskeleton of the dorsal fin consists of several radials, each including two ossifications, viz. an axonost and a baseost. The axonost is long and circular in cross section and the anterior axonosts articulate direct with the basidorsals. The hindmost axonosts appear to be continuous with the basidorsals. The baseosts are small and rather hour-glass shaped. There are no distal ossifications beyond them as described by Nielsen (1942 : 243) in *Pteronisculus aldingeri* (Nielsen). Nothing more of the dorsal fin support could be made out and it was impossible to decide if there was a large plate in the axonost series as in *Pteronisculus aldingeri* (Nielsen).

The endoskeleton of the anal fin is far more satisfactorily preserved (R.S.M. 1950.38.87). It consists of a single series of radials numbering probably sixteen, which are longest in the anterior region and become successively shorter posteriorly (Text-fig. 8). These radials probably represent the fusion of two elements, the baseosts and axonosts, to give a single ossification. In *Pygopterus nielseni* Aldinger (1937, fig. 42) similarly only one series of ossifications is found in the endoskeleton of the anal fin. In *Pteronisculus* there are two ossifications and it seems likely that the distal series here must represent ossifications in the distal radial segments, a tentative suggestion already put forward by Nielsen (1942 : 249).

*The axial skeleton.* Anterior to the dorsal fin several basidorsals can be made out ; these consist of a small, four-sided proximal plate and a distal process. An independent supraneural, associated with the distal process, can be made out in one instance.

Above the radials of the anal fin occur a series of ossifications associated with the notochord. These ossifications consist of a basiventral which has become fused with the unpaired infrahaemals. These haemal arches become progressively longer posteriorly. From the distance apart of these haemal arches in the posterior region it seems probable that they alternated with small intraventrals as in *Pteronisculus aldingeri* (Nielsen).

The remaining ossifications in the caudal region are very similar to those described by Nielsen (1942 : 216) for *Pteronisculus aldingeri* (Nielsen), with the unpaired distal parts of the haemal arches being widened so as to form hypurals, which possibly include radial elements. Dorsally in the caudal region there is but a single series of basidorsal elements. Nothing further of the axial skeleton could be determined with any degree of certainty.

*Squamation.* The scales have been well described by Traquair (1909 : 118), and are peculiar in form. The scales in the flank regions are much higher than broad and the exposed area is more or less rhomboidal, but as Traquair points out "the acute angles are here the postero-superior and the antero-inferior". The scales are only very slightly imbricating and the ornamentation consists of delicate



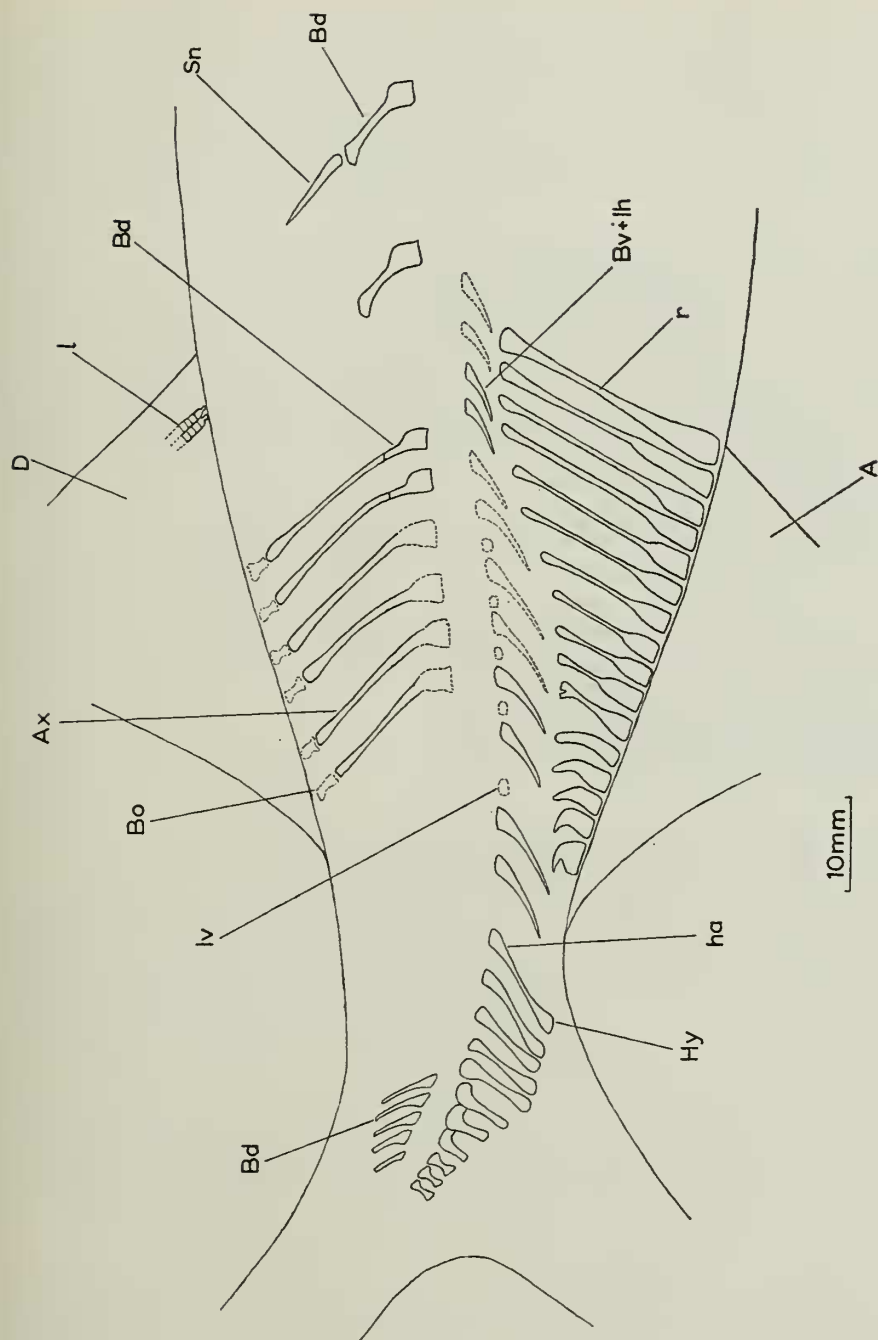


FIG. 8. *Nematopterychius greenochi* (Traquair). Axial skeleton. Mainly from R.S.M. 1890.78.4, 1889.5.1 and 1950.38.87.

wavy ridges, branching and anastomosing and directed obliquely downwards. The scales on the ventral part of the body are very small and equilateral in shape. On one specimen (B.M.N.H., P.11558) where that region showed at all clearly I have observed a small patch of smaller scales beneath the posterior end of the dorsal fin which is not continuous with the normal scale rows. In this *N. greenocki* shows something approaching the condition seen in *Pygopterus nielsenii* Aldinger (1937, fig. 37).

### Family RHABDOLEPIDAE nov.

DIAGNOSIS. As genus for the *Rhabdolepis*.

REMARKS. From my description of *Rhabdolepis* it is clear that this genus does not belong in the family Elonichthyidae, where both Aldinger (1937 : 376) and Romer (1945 : 579) placed it ; further it does not fit into any other previously described family. A new family, Rhabdolepidae, is therefore erected to include this single genus.

From the scale structure, body form and disposition of the fins, the family Rhabdolepidae seems fairly close to the family Elonichthyidae.

### Genus RHABDOLEPIS Troschel, 1857

- 1829 *Palaeoniscum* Bronn, *partim*, p. 483.
- 1833 *Amblypterus* Agassiz, *partim*, 2, 1, pp. 4, 37.
- 1873 *Leiolepis* Goldenberg, p. 5 (name only).
- 1891 *Elonichthys* Woodward, *partim*, p. 491.
- 1905 *Pygopterus* Langenhan, p. 10.

DIAGNOSIS (emended). Trunk deeply fusiform ; dorsal fin partly in advance of, partly opposing the anal, both large, acuminate and distinctly triangular, anal slightly larger than dorsal. Caudal fin powerful, deeply cleft and heterocercal. Paired fins large, pelvic pair smaller than pectorals, arising midway between the latter and the anal. All fins with minute fulcra anteriorly and with rays articulated and distally bifurcating. Skull with oblique suspensorium, prominent rostrum and delicate sclerotic ring. Opercular long and very narrow and with accessory opercular separating it completely from subopercular. Suborbital series present and branchiostegal rays numerous ; skull roofing bones ornamented with tubercles, other skull bones striated. Dentition consisting of inner series of large, stout, conical laniaries, few in number, and outer series of much smaller and far more numerous teeth ; scales small, as broad as deep on flank, ornamented with irregular, delicate, oblique striae, terminating as series of digitations on anterior overlapped border. On flank scales, three or four striae run nearly parallel with inferior scale border.

TYPE SPECIES. *Palaeoniscum macropterus* Bronn.

REMARKS. The type species was first assigned to the genus *Palaeoniscum* by Bronn (1829 : 483), but Agassiz (1833 : 3) realizing that it did not in fact belong to this genus, placed it in a new genus *Amblypterus*. He also (Agassiz, 1833 : 4)

listed several species to be included within the genus *Amblypterus*, but did not designate any one of them as the type species.

Troschel (1857 : 15) decided that *Amblypterus macropterus* Agassiz, *Amblypterus eupterygius* Agassiz, *Amblypterus striatus* Agassiz, *Amblypterus agassizii* Münster and *Amblypterus ornatus* Giebel on their dentition were very different from all the other species placed in the genus *Amblypterus* by Agassiz, so he removed them and founded the genus *Rhabdolepis* for their reception, but like Agassiz he omitted to designate any one of them as the type species of his new genus *Rhabdolepis*. However, Sauvage (1888 : 59) quite correctly designated *Amblypterus macropterus* Agassiz as the type species of the genus *Rhabdolepis* Troschel even though he incorrectly attributed the species to Agassiz instead of to Bronn.

Thus *Palaeoniscum macropteron* Bronn must be regarded as the type species of the genus *Rhabdolepis* Troschel.

My reason for dealing in this paper with an essentially Permian genus is that like *Watsonichthys* Aldinger and *Cosmoptychius* Traquair it possesses an accessory opercular bone. This accessory opercular bone, however, completely separates the opercular from the subopercular and this condition is very similar to that described by Casier (1952, text-fig. 1) in *Osorioichthys marginis* (Casier) from the Devonian. What Casier (1952, text-fig. 1) labelled subopercular in fact corresponds to the accessory opercular in *Rhabdolepis macropterus* (Bronn) (Text-fig. 9) and what he termed the first branchiostegal ray is undoubtedly the true subopercular, and thus his argument that this first branchiostegal in *Osorioichthys marginis* is equivalent to the interopercular in higher fishes is completely erroneous. [Note : Casier originally described this fish as *Stereolepis marginis* n. gen., n. sp.; however the genus was already preoccupied so he (1954) erected the new genus *Osorioichthys* for its reception.]

### *Rhabdolepis macropterus* (Bronn)

(Text-fig. 9)

- 1829 *Palaeoniscum macropteron* Bronn, pp. 483, 493.
- 1833 *Amblypterus macropterus* (Bronn) Agassiz, 2, 1, pp. 4, 31, pl. 1, figs. 4-7, pl. 3, figs. 1-4.
- 1833 *Amblypterus eupterygius* Agassiz, 2, 1, pp. 4, 36, pl. 1, fig. 8, pl. 3, figs. 5, 6.
- 1847 *Amblypterus macropterus* Agassiz : Goldfuss, p. 20, pl. 5, figs. 1-8.
- 1848 *Amblypterus macropterus* Agassiz : Giebel, p. 252.
- 1848 *Amblypterus eurypterygius* Agassiz : Giebel, p. 253.
- 1857 *Rhabdolepis macropterus* (Agassiz) Troschel, p. 15, pl. 2, fig. 15.
- 1857 *Rhabdolepis eupterygius* (Agassiz) Troschel, p. 15, pl. 2, fig. 14.
- 1873 *Amblypterus eupterygius* Agassiz : Goldenberg, 1, p. 5, pl. 1, fig. 2.
- 1877b *Rhabdolepis macropterus* (Bronn) : Traquair, p. 552.
- 1877c *Rhabdolepis macropterus* (Bronn) : Traquair, pl. 2, fig. 6.
- 1888 *Rhabdolepis macropterus* (Agassiz) : Sauvage, p. 59.
- 1891 *Elonichthys macropterus* (Bronn) Woodward, p. 491.
- 1892 *Amblypterus traquairi* Pohlig, p. 63, pl. 7, fig. 4.
- 1905 *Amblypterus* sp., Langenhan, pp. 9, 11, pl. 1c, fig. 17, pl. 1e, figs. 1, 4a, b.
- 1905 *Pygopterus antiquus* Langenhan, pp. 10, 11, pl. 1e, figs. 3a, b, pl. 1c, figs. 10-14, 16.
- 1905 *Amblypterus duvernoyi*? (Agassiz) : Langenhan, p. 10, pl. 1e, fig. 1.
- 1905 *Amblypterus traquairi* Pohlig : Langenhan, p. 10, pl. 1e, figs. 2a, b, pl. 3, fig. 4, pl. 4, figs. 2, 5, pl. 6, fig. 5.

- 1905 *Amblypterus elegans* Langenhan, p. 11, pl. 1e, figs. 5a, b, pl. 2, fig. 2.  
 1905 *Amblypterus gracilis* Langenhan, p. 11, pl. 2, fig. 1, pl. 4, fig. 6.  
 1905 *Amblypterus elongatus* Langenhan, p. 11, pl. 2, fig. 3, pl. 6, fig. 1.  
 1905 *Amblypterus regelii* Langenhan, p. 11, pl. 5, fig. 1.  
 1905 *Rhabdolepis macropterus* (Bronn) : Langenhan, p. 12, pl. 6, fig. 4.  
 1937 *Rhabdolepis macropterus* (Bronn) : Aldinger, p. 209.

DIAGNOSIS (emended). A species of moderate to large size, but not exceeding 40 cm. in total length. Length of head nearly equal to maximum depth of trunk and contained about four and a half times in total body length. Both dorsal and anal fins large, triangular and concavely cut out behind. Lepidotrichia of fins longitudinally striated. Opercular completely separated from subopercular by accessory opercular. Scales in anterior trunk region with delicately denticulated hinder margin, while ornamentation finishes in series of digitations on anterior overlapped border. Further back on trunk region hinder margins of scales without serrations. Probably three ridge-scales in front of dorsal fin, two in front of caudal fin and three very large ones in front of anal fin ; ridge-scales on axial lobe of tail commence just behind dorsal fin.

SYNTYPES. *Olim* H. G. Bronn Collection, from the Lower Permian of Saarbrück, Lebach and Boerschweiler, Germany. Searching the literature and contacting many German Museums has failed to reveal what was the subsequent fate of the Bronn Collection, thus I propose as the neotype B.M.N.H., P.3453 and counterpart P.2072, nearly complete fish from the Lower Permian, Lebach, Germany.

MATERIAL. Specimens from the British Museum (Natural History) and the Stuttgart Museum. Approximately twenty-five specimens were examined.

REMARKS. It was Troschel (1857 : 15) who first realized that *Amblypterus macropterus* (Bronn) did not agree in structure with the other species assigned to the genus *Amblypterus* by Agassiz (1833 : 4) and founded the new genus *Rhabdolepis* for its reception. Traquair (1877b : 552) followed Troschel in keeping *Amblypterus macropterus* (Bronn) in the genus *Rhabdolepis*. Woodward (1891 : 437, 491) also realised that this species did not belong to the same genus as *Amblypterus latus* Agassiz, but put *macropterus* Bronn in the genus *Elonichthys* Giebel. Aldinger (1937 : 209) correctly recognized that *macropterus* Bronn, on the nature of the opercular apparatus alone, did not belong to *Elonichthys*, and resurrected Troschel's genus *Rhabdolepis* for its reception.

From my description it is clear that *Palaeoniscum macropterus* Bronn was correctly placed in the genus *Rhabdolepis* by Troschel.<sup>1</sup>

DESCRIPTION. *The skull.* The shape and arrangement of the dermal bones of the skull are shown in Text-fig. 9. The most characteristic features are the accessory opercular completely separating the opercular from the subopercular, the delicate sclerotic ring and the presence of a rostrum.

The skull roofing bones are ornamented mainly with tubercles, but also with a

<sup>1</sup> Acanthodian remains are frequently found in the abdominal cavity of some of the larger specimens of this species.

few very short ridges of enamel. On the suprascapulars, extrascapulars, parietals, frontals, dermopterotics, dermosphenotics and nasals the tubercles run more or less from the ossification centres of these bones to their edges. The infraorbitals and antorbital bones are also tuberculated, but the remainder of the skull bones are delicately striated. On the maxilla the fine ridges of enamel run for a short distance upwards and forwards from the postero-ventral corner, but on the remainder of that bone the ridges follow the outline more closely. On the preopercular the ridges follow the length of the bone, whilst on the suborbitals, opercular, subopercular and accessory opercular they run more concentrically.

The ornamentation of the lower jaw consists of longer but finer ridges which run along the length of the bone dividing and anastomosing occasionally. On the branchiostegal rays and median gular the ridges are very delicate.

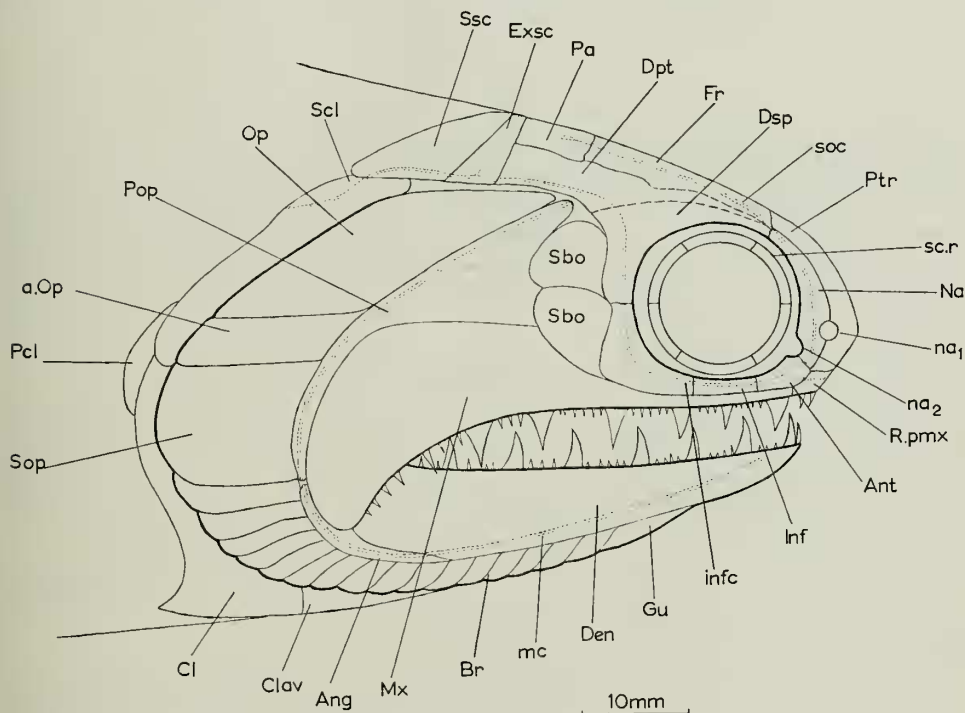


FIG. 9. *Rhabdolepis macropterus* (Bronn). Reconstruction of skull in lateral view.

The skull itself is long with an oblique suspensorium and the orbit situated well forwards. The single pair of triangular suprascapulars meet in the midline and are preceded by the normal pair of extrascapulars. The parietals are square and the frontals rectangular. Anteriorly the frontals join the postrostral and the nasals. The lateral wall of the skull is made up of the dermopterotic and the dermosphenotic, but this area is badly preserved in all the specimens I have examined and thus the true extent of these two bones can only be guessed at. Ventrally the nasal joins



the antorbital. This latter bone forms the lower edge of the posterior nostril (see B.M.N.H., P.992). Anterior to the antorbital and beneath the postrostral lies a pair of small rostro-premaxillaries. The rostro-premaxillary is not often observed but it can be seen displaced in front of the snout in specimen B.M.N.H., P.993, where it bears several small pointed teeth. Between the antorbital and the dermosphenotic are two members of the infraorbital series, the posterior one being much the larger. The maxilla is long and narrow and bears teeth along the whole of its ventral margin. These teeth are in two series, a set of very large, pointed teeth and a series of far more numerous, much smaller ones. The preopercular is high and broad and anteriorly the margin is twice scalloped out for the reception of the two suborbital bones. The opercular apparatus is narrow and the accessory opercular completely separates the opercular from the subopercular. There are about sixteen branchiostegal rays and a small lozenge-shaped median gular. The orbit contains a delicate sclerotic ring composed of six segments (see B.M.N.H., P.6196).

*Lower jaw.* The lower jaw is made up of a stout angular posteriorly and with a large dentary forming the remainder of the outer surface. The dentary also forms part of the inner jaw surface anteriorly. The remainder of the inner surface is covered by a large prearticular. The upper border of the dentary supports a series of very large conical pointed teeth and an outer row of numerous, closely arranged, small teeth. These are set on a shelf which is overlapped by the coronoid. The tooth bearing surface of the jaw is almost flat, and posteriorly the articular portion of Meckel's cartilage is ossified.

*Palate.* Little could be made out of the palate apart from there being an ossified quadratojugal bone present, which enters partly into the jaw articulation.

*The paired fins and their girdles.* The pectoral girdle is of the normal palaeoniscoid pattern and contains a single postcleithrum. The dermal bones are delicately ornamented with short striae which run along the length of the bones. There are ossified radials, four or five in number, and the lepidotrichia of the fin number between twenty and twenty-five. All the rays are articulated to their bases.

The pelvic fin is smaller than the pectoral and is composed of fifteen to twenty rays. Both the pectorals and pelvics are fringed anteriorly with very small fulcral scales.

*The unpaired fins.* The dorsal and anal fins are large, distinctly triangular, and concave posteriorly. The dorsal fin is the smaller of the two with from thirty-eight to forty rays, while the anal has between forty-five and fifty lepidotrichia. However, there seems to be considerable variability in numbers of fin rays within this species. The caudal fin is heterocercal, deeply cleft and nearly equilobate.

The endoskeleton of the dorsal fin consists of about seventeen radials, each composed of two separate ossifications, an axonost and a baseost. The baseosts can clearly be seen on B.M.N.H., P.14537 and P.993a; they are hour-glass shaped and diminish gradually in size from before backwards. These baseosts are much larger than those in *Nematoptychius greenocki* (Traquair). The axonosts are much longer and appear to be continuous with the neural spines.

The exoskeleton of the anal fin is also often preserved. It consists of about fifteen radials and although it could not be verified it would appear that these radials consist of two ossifications (B.M.N.H., P.15098), a long axonost and a much shorter hour-glass shaped baseost (B.M.N.H., P.6196).

*Squamation.* The scales are relatively small and about as broad as they are deep on the flank. They are delicately ornamented with oblique striae, which cross the scale surface from the antero-superior corner to the postero-inferior corner. These striae occasionally anastomose, and they finish as a series of digitations on the anterior overlapped border. On the flank scales three or four of these striae at the anterior border run almost parallel to that border.

***Rhabdolepis saarbrueckensis* n. sp.**

(Text-fig. 10)

1891 *Elonichthys macropterus* (Bronn) : Woodward, p. 493.

**DIAGNOSIS.** A species closely resembling the type species except that there are two accessory opercular bones separating the opercular from the subopercular (Text-fig. 10). Probably four ridge-scales in front of dorsal fin and not three as in *Rhabdolepis macropterus* (Bronn).

**HOLOTYPE.** B.M.N.H., 32576 in counterpart, from the Lower Permian of Saarbrück. The only specimen seen.

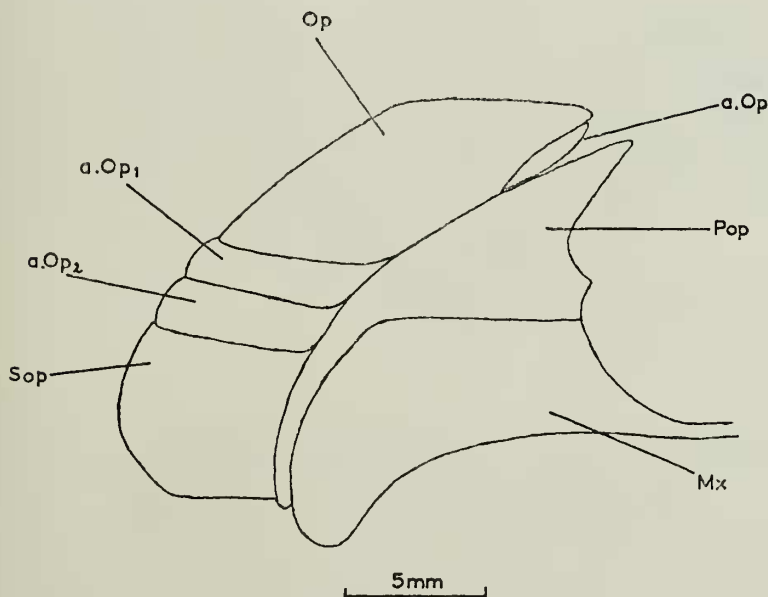


FIG. 10. *Rhabdolepis saarbrueckensis* n. sp. Cheek and opercular apparatus, lateral view.

REMARKS. Woodward (1891 : 493) lists specimen No. 32576 under *Elonichthys macropterus* (Bronn) ; however from the facts given above it clearly belongs to a separate species which I have called *saarbrueeckensis* after the locality where it was found.

DESCRIPTION. This species only differs from the type in the points already cited of which the most significant is the presence of a second accessory opercular bone (a.Op.<sub>2</sub>, Text-fig. 10) lying immediately beneath the first accessory opercular bone.

### Family AMBLYPTERIDAE Romer

1954 Romer, p. 579 (name only).

DIAGNOSIS (emended). Trunk deeply fusiform ; dorsal fin partly in advance of, partly opposing, anal fin ; both large, triangular and approximately same size. Dorsal contour much arched in advance of dorsal fin. Paired fins large or of moderate size. All fins with fulcra anteriorly and with rays articulated and distally bifurcating. Suspensorium almost vertical, rostrum only feebly developed if at all. Opercular larger than subopercular. Dermohyal and suborbital series present, branchiostegal rays few and teeth minute.

REMARKS. I have used this family to include the genus *Amblypterus*, but it would seem that the two genera, *Paramblypterus* Sauvage and *Amblypterygia* Berg also belong to this family (as already suggested by Romer, 1945 : 579). Since this paper was written, due to the kindness of Professor J. P. Lehman I have been allowed to read an as yet unpublished thesis entitled : *Étude des Palaeoniscidés du Bassin Houiller de Commentry (Allier)* by Jacques Blot. This has further confirmed my belief that *Paramblypterus* Sauvage [which Blot has shown to include *Amblypterygia* Sauvage, *Geomichthys* Sauvage, *Cosmopoma* Sauvage and *Dipteroma* Sauvage] should be placed in the Amblypteridae, while *Commentrya* Sauvage [shown by Blot to include *Elaveria* Sauvage], which Romer (1945 : 579) also placed in this family, must clearly be removed and put into a family of its own, the Commentryidae, *fam. nov.* (a family fairly close to both the Elonichthyidae and the Amblypteridae).

### Genus AMBLYPTERUS Agassiz

1833 *Amblypterus* Agassiz, *partim*, **2**, 1, pp. 4, 37.

1833 *Palaeoniscus* Agassiz, *partim*, **2**, 1, pp. 4, 45, 103.

1873 *Leiolepis* Goldenburg, p. 5 (name only).

1890 *Aedua* Sauvage, p. 16.

1890 *Archeoniscus* Sauvage, p. 19.

DIAGNOSIS (emended). Trunk deeply fusiform ; dorsal fin partly in advance of, partly opposing, anal fin ; both large, triangular and approximately same size. Dorsal contour much arched in advance of dorsal fin. Paired fins large or of moderate size, pelvic pair placed slightly nearer to anal than to pectorals. All fins with minute fulcra anteriorly and with rays articulated and distally bifurcating. Skull with almost vertical suspensorium, slight rostrum and delicate sclerotic ring. Opercular not quite twice as large as subopercular, suborbital series and dermohyal present. Branchiostegal rays few, skull roofing bones coarsely striated. Teeth



minute and in one series. Scales large and smooth except sometimes in anterior abdominal region and immediately behind ventral portion of pectoral girdle where they exhibit a few delicate striae.

TYPE SPECIES. *Amblypterus latus* Agassiz.

REMARKS. As already pointed out under remarks on the genus *Rhabdolepis* (p. 284), Agassiz (1833 : 4) in erecting the genus *Amblypterus* listed several species without designating any one as the type species. Troschel (1857 : 18) later removed several of these species and put them in the new genus *Rhabdolepis*. However, from the remaining species Sauvage (1888 : 58) subsequently correctly designated *Amblypterus latus* Agassiz as the type species of the genus *Amblypterus*. Woodward (1891 : 437) also came to this conclusion, but for somewhat different reasons.

### *Amblypterus latus* Agassiz

(Text-fig. 11)

1833 *Amblypterus latus* Agassiz, **2**, 1, pp. 4, 37, pl. 4, figs. 2-6.

1833 *Amblypterus lateralis* Agassiz, **2**, 1, pp. 4, 39, pl. 4, figs. 1, 7-9.

1857 *Amblypterus latus* Agassiz : Troschel, p. 13, pl. 2, fig. 17.

1877b *Amblypterus latus* Agassiz : Traquair, p. 552.

1877b *Amblypterus lateralis* Agassiz : Traquair, p. 552.

1877c *Amblypterus latus* Agassiz : Traquair, pl. 2, fig. 1.

1888 *Amblypterus latus* Agassiz : Sauvage, p. 58.

1891 *Amblypterus latus* Agassiz : Woodward, p. 437.

1925 *Amblypterus* sp., Watson, p. 824, text-fig. 4.

1937 *Amblypterus latus* Agassiz : Aldinger, p. 217, text-fig. 57.

DIAGNOSIS (emended). A species reaching 20 cm. in total length. Length of head contained about four times in total body length and over one and a half times in maximum depth of trunk. Both dorsal and anal fins large, longer than deep and origin of dorsal behind middle point of back. Anal fin opposed to hinder two-thirds of dorsal. Paired fins also large, pelvic pair smaller than pectoral. Scales large and smooth, caudal pedicle short and robust. Three large ridge scales in front of dorsal fin, two in front of anal fin and three in front of caudal. Dorsal ridge scales extend back from tail almost to dorsal fin.

HOLOTYPE. Part and counterpart of a nearly complete fish in the Strassburg Museum, figured by Agassiz (1833, text-figs. 2, 3) from the Lower Permian of Saarbrück, Germany.

MATERIAL. Specimens from the British Museum (Natural History). Eighteen specimens examined.

REMARKS. A redescription of the type species of the genus *Amblypterus* (*A. latus*) is given below so that the many species which have been placed in this genus by a number of workers may now be more satisfactorily compared.

DESCRIPTION. *The skull.* The general shape of the skull can be seen from Text-fig. 11. The snout is rounded with but a slight protuberance which is nothing like the rostrum seen in *Elonichthys* Giebel or even as marked as in *Rhabdolepis* Troschel. The roofing bones of the skull are ornamented with coarse tubercles

and ridges of enamel. These ridges are most pronounced on the suprascapulars, extrascapulars, parietals, frontals, dermopterotics, dermosphenotics, nasals and postrostral bones, where they follow the length of the bone. The remaining skull bones are much more delicately ornamented; on the opercular and subopercular and suborbitals delicate striae run concentrically round the bones whilst the maxilla, preopercular, infraorbitals, antorbital, branchiostegal rays and lower jaw are almost smooth.

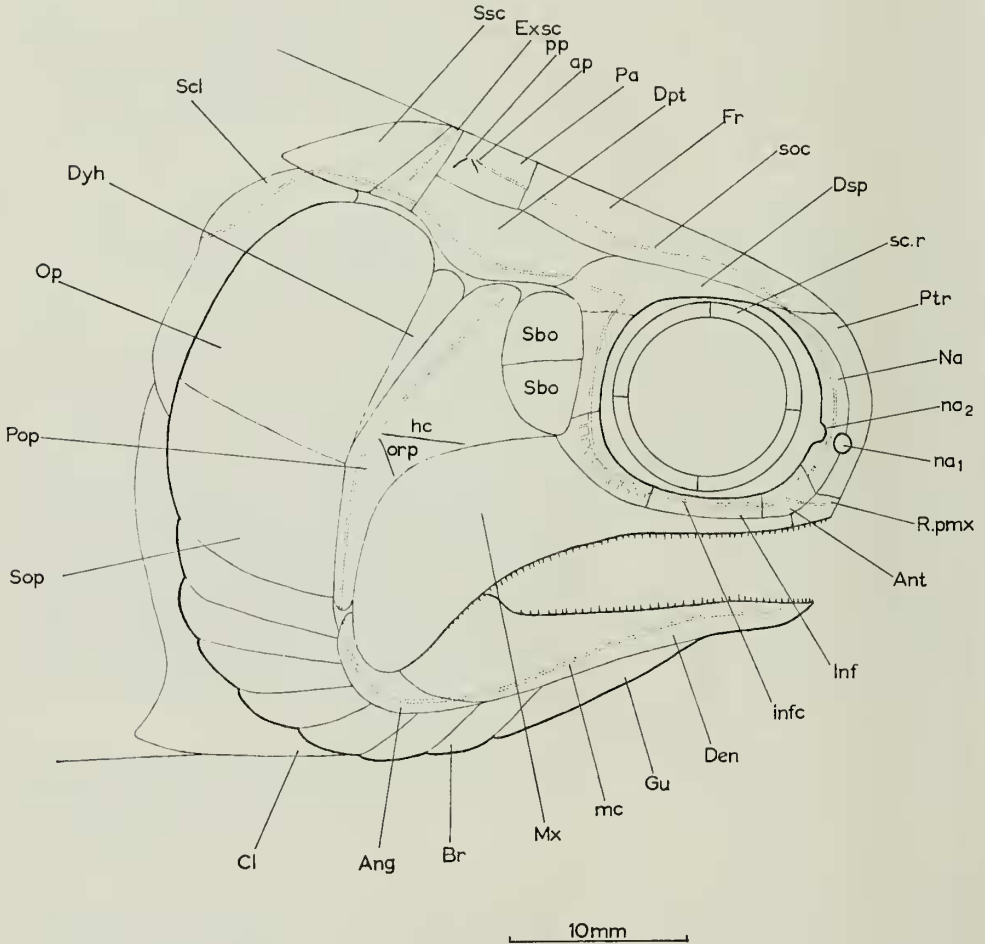


FIG. 11. *Amblypterus latus* Agassiz. Reconstruction of skull in lateral view.

The skull itself is short with an almost vertical suspensorium. The suprascapulars are distinctly triangular and their anterior edge is longer than their lateral border. The extrascapular series consists of the normal single pair of bones and is preceded

by the almost square parietals. The frontals are the longest bones in the skull roof and anteriorly meet both the postrostral and the nasals. The lateral wall of the roof is composed of a dermopterotic which is preceded by a large dermosphenotic. The antero-lateral edge of the dermosphenotic forms part of the upper limit of the orbit, and anteriorly it meets the nasal. Both the postrostral and the nasal bones are long and the postrostral is only moderately convex anteriorly. Ventrally the nasal joins the small antorbital. In front of the maxilla and beneath the postrostral there is evidence of a small rostro-premaxillary (see B.M.N.H., P.145366). There are three members of the infraorbital series and the infraorbital sensory canal gives off numerous, posteriorly directed branches in the second member. The maxilla is of normal palaeoniscoid pattern, but anteriorly the lower margin turns slightly upwards, which, together with the position of the rostro-premaxillary, gives a slight upturning to the snout. The teeth on the maxilla are very small and of one series only. The preopercular is relatively narrow and much nearer the vertical than in any of the other forms so far described in this paper, in fact the preopercular is very similar in shape to that seen in *Mesopoma pulchellum* (Traquair) (Moy-Thomas & Dyne, 1938, text-fig. 9). The anterior margin of the preopercular is convex where the two members of the suborbital series fit into it. Both suborbitals are of roughly the same size and shape. On the preopercular both the vertical and horizontal pit lines can be clearly seen on many of the specimens. Between the preopercular and the opercular is a wedge-shaped dermohyal. The opercular is over one and a half times deeper than the subopercular. Preceding the subopercular are seven broad branchiostegal rays and a large median gular. The orbit is supported by a delicate sclerotic ring, composed probably of four elements; bits of this ring can be seen on specimens B.M.N.H., P.6195a, P.3458a and P.978.

*Lower jaw.* The posterior third of the lower jaw is over twice as deep as the remainder. Anteriorly the jaw is very shallow. The angular bone does not extend very far along the ventral jaw surface and only the articular region of Meckel's cartilage is ossified. The dentary, where it turns under and up to form part of the inner surface of the jaw, is considerably thickened, giving a very stout keel to the lower inner surface. There are three members of the coronoid series, all of which bear small tubercles on their dorsal surface. The lower jaw is well shown on B.M.N.H., 44082 and on one specimen of *Amblypterus duvernoyi* (Agassiz) B.M.N.H., P.21987 which is very similar to *A. latus*.

*The paired fins and their girdles.* The pectoral girdle consists of a supracleithrum which stretches down to beyond the junction of the opercular and subopercular, an elongate cleithrum and a stout clavicle. The ornamentation is more pronounced on the supracleithrum and cleithrum than on the opercular series. It consists of elongate striae of enamel which follow more or less the long axis of the bone. The pectoral fin is large, with a longish base line; there are four or more ossified radials present and the lepidotrichia of the fin number between twenty-five and twenty-eight. All the rays are articulated to their bases.

The pelvic fin is also large, a little smaller than the pectoral, having some twenty lepidotrichia. The base line is long and the rays in the middle region of the fin are

very stout. Both the paired and unpaired fins are fringed anteriorly with small fulcral scales.

*The unpaired fins.* The dorsal and anal fins are large, triangular and, contrary to Woodward (1891 : 438), deeper than they are long. Both fins are of comparable size with twenty-eight to thirty-two lepidotrichia. The tail is heterocercal, deeply cleft and inequilateral.

*Squamation.* The scales are large and smooth, those in the middle of the flank not much deeper than broad.

#### Family **STEGOTRACHELIDAE** nov.

**DIAGNOSIS.** Trunk deeply fusiform ; mandibular suspension moderately oblique to oblique ; caudal pedicle robust ; maximum depth of body contained about four times in total length. Dorsal and anal fins opposing one another, caudal fin heterocercal. Prominent dorsal and ventral ridge scales in at least the Devonian members. Paired fins small with intervals between articulations in lepidotrichia long. Snout with poorly developed rostrum, generally composed of three bones only, median postrostral, paired nasals and rostro-premaxillo-antorbitals. Frontals nearly always pierced by pineal foramen. Ornamentation of skull roofing bones consisting of fine ridges of enamel which follow the length of the bones. Scales ornamented with diagonal ridges which often end on posterior scale margins as series of serrations.

**REMARKS.** I have erected this family to include the two Devonian genera *Stegotrachelus* (Woodward & White, 1926) and *Moythomasia* (Gross, 1942, 1953), and the Lower Carboniferous genus *Kentuckia* (Rayner, 1951).

Gross (1933b, 1942) has suggested that *Stegotrachelus* is congeneric with *Moythomasia* although Rayner (1951 : 55) thinks this unlikely. From the following description of *Stegotrachelus* it is clear that the two genera are quite separate, but on the other hand are close enough to be grouped in the same family.

Rayner (1951 : 54, 75) has shown that *Kentuckia* is also closely related to *Moythomasia* and as such it too may be included in the family Stegotrachelidae.

#### Genus **STEGOTRACHELUS** Woodward & White, 1926

**DIAGNOSIS.** See Woodward & White, 1926 : 567.

**TYPE SPECIES.** *Stegotrachelus finlayi* Woodward & White.

**REMARKS.** Since Gross (1942) has suggested that *Stegotrachelus* is congeneric with *Moythomasia* a re-examination of *Stegotrachelus* can profitably be undertaken. Of the six Devonian genera of actinopterygians so far described *Cheirolepis* Agassiz, *Tegeolepis* Miller, *Stegotrachelus* Woodward & White, *Moythomasia* Gross, *Osorioichthys* Casier and *Orvikuina* Gross, two are known only by scales and of the remainder only the skulls of *Cheirolepis* Agassiz and *Moythomasia* are at all well known.

*Stegotrachelus finlayi* Woodward & White  
(Text-fig. 12)

1926 *Stegotrachelus finlayi* Woodward & White, p. 568, pl. 3.

1937 *Stegotrachelus finlayi* Woodward & White : Aldinger, p. 298, text-fig. 90.

DIAGNOSIS. See Woodward & White (1926 : 567) with the following emendments :—(1) There is no suborbital series present. (2) The frontal is pierced by a pineal foramen. (3) The snout has a slight rostrum and is composed of three bones only, median postrostral, paired nasals and rostro-premaxillo-antorbitals.

HOLOTYPE. Nearly complete fish (B.M.N.H., P.13407) from the Middle Old Red Sandstone of Exnaboe, Shetland.

MATERIAL. Specimens from the British Museum (Natural History) (including the type) and from the Royal Scottish Museum. Twelve specimens in all.

REMARKS. This is the only species of this genus so far described. The general form of the body and fins have been well described and figured by Woodward & White (1926 : 568) but a more detailed study of the head is clearly needed. In the last few years new material of *Stegotrachelus finlayi* has been collected by Mr. H. Crawford and presented to the British Museum (Natural History) and this, together with the old material, has made the following description possible.

DESCRIPTION. *The skull.* The skull roofing bones are well shown in B.M.N.H., P.13410, P.20309 and P.45056. The suprascapular series consist of a single pair of bones which are large, triangular, and can be seen displaced in B.M.N.H., P.13413. The extrascapular series is made up of a single pair of very narrow bones much as in *Moythomasia nitida* Gross, but the square parietals succeeding them are smaller by comparison than those in *Moythomasia*. The frontals can clearly be seen in B.M.N.H., P.13410, P.20309 and P.45056, where they are pierced anteriorly by a large pineal foramen as in *Moythomasia perforata* (Gross). The lateral wall of the skull roof is composed of the dermosphenotic and dermopterotic. The dermosphenotic lies anteriorly to the dermopterotic (see B.M.N.H., P.13410 and P.45056), as in *Moythomasia perforata* and *Kentuckia deani* (Eastman), and it does not take part in the formation of the orbital border. Anteriorly the dermosphenotic joins the nasal.

The postrostral has a broad "V"-shaped insertion between the anterior extremities of the frontals, just anterior to the pineal foramen, again a very similar condition is seen in *Moythomasia perforata* (B.M.N.H., P.20309 for the anterior extremities of the frontals and P.13410 for the postrostral). The postrostral is long and the nasals which lie alongside it are of about the same length. The nasals are notched for the anterior and posterior nostrils, these notches being clearly observable on B.M.N.H., P.20310. The bone lying along the posterior margin of the nasal in P.13410 is the displaced nasal from the other side, not a circumorbital as figured by Woodward & White (1926, text-fig. 7, pl. 3, fig. 5). The postrostral curves sharply just at the point where the nares open on to the external surface (see B.M.N.H., P.20310). Beneath the postrostral and nasals lie the paired rostro-



premaxillo-antorbital. The rostro-premaxillo-antorbital bears teeth along its ventral margin and although fragmentary can just be made out on B.M.N.H., P.13410 and P.13407.

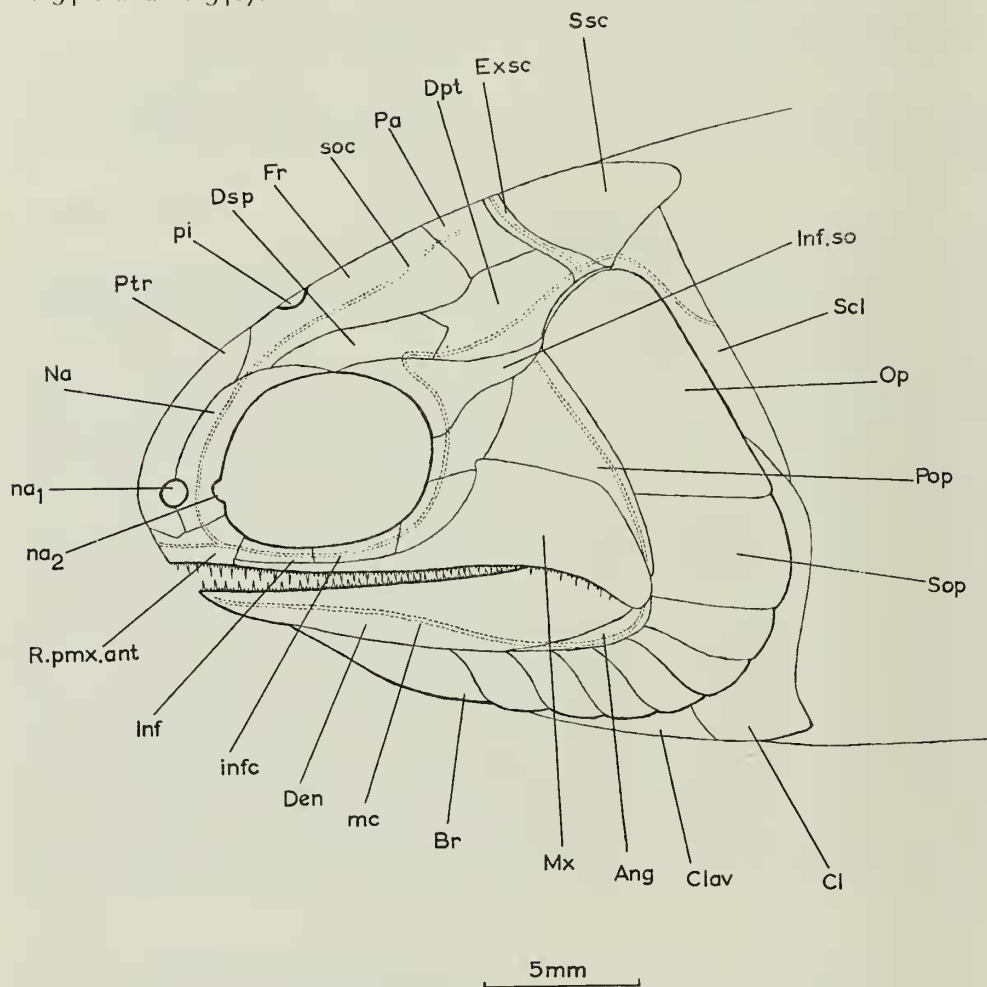


FIG. 12. *Stegotrachelus finlayi* Woodward & White. Reconstruction of skull in lateral view.

Bounding the orbit below and behind are four members of the infraorbital series, the fourth, the most dorsal member being the largest (B.M.N.H., P.13407, P.13410 and P.13416). Dorsally the fourth infraorbital meets the infraorbital-supraorbital (B.M.N.H., P.13410 and P.13416). The infraorbital-supraorbital posteriorly meets the preopercular, dorsally both the dermopterotic and dermosphenotic and anteriorly the nasal. It is the same bone as that called postorbital by Rayner (1951, text-fig. 2) in *Kentuckia deani* and that labelled postfrontal in *Cheirolepis trailli* Agassiz (Watson,

1925 : 817), as Rayner (1951 : 57) has already pointed out. A similar bone is also found in *Nematoptychius greenocki* (Text-fig. 5).

The maxilla is of the normal palaeoniscoid pattern and bears a double series of teeth along its entire ventral margin. The teeth are delicate and there is a series of larger teeth interspersed with a series of more numerous, much smaller teeth. The preopercular (B.M.N.H., P.13410, P.13407 and P.13409) is of rather unusual shape in so much as its dorsal extremity is notched for the reception of the posterior end of the infraorbito-suborbital. The opercular is nearly upright, over twice as high as it is broad and over twice as high as the subopercular. The branchiostegal rays are few in number (seven) and the most anterior pair are very large.

*Lower jaw.* The lower jaw is composed of a long dentary bone which forms almost all of the outer jaw surface, with the posterior jaw margin made up of a narrow angular. The dentary also forms almost the whole of the inner jaw surface anteriorly and is overlain by a long flat prearticular. The articular region of Meckel's cartilage is ossified and so too is the following third. Whether or not other elements such as coronoids and surangular existed could not be ascertained. The dentary, like the maxilla, bears a large number of teeth of two sizes. Of the other skull bones, palate, neurocranium, etc., little could be made out.

REMARKS. The Upper Devonian of North America has yielded the following palaeoniscoid species :— *Palaeoniscus devonicus* Clarke, *Palaeoniscus reticulatus* Williams, *Palaeoniscus antiquus* Williams and *Actinophorus clarki* Newberry. These were all described prior to 1900 and since that time only Hussakof & Bryant (1918) and Gross (1933, 1953) appear to have more than just mentioned any of them. As Devonian forms they are obviously of considerable importance, thus I am describing them below in their appropriate genera. The first three species, *P. devonicus* Clarke, *P. reticulatus* Williams and *P. antiquus* Williams belong to the genus *Moythomasia* Gross but the fourth, *A. clarki* Newberry, belongs to a separate genus and family (Tegeolepididae).

#### Genus *MOYTHOMASIA* Gross, 1950

1942 *Aldingeria* Gross, p. 431.

DIAGNOSIS. See Gross, 1942 : 430.

TYPE SPECIES. *Moythomasia perforata* (Gross).

#### *Moythomasia devonica* (Clarke)

1879 *Palaeoniscus* sp., Hinde, p. 353.

1885 *Palaeoniscus devonicus* Clarke, pp. 20, 41, pl. 1, figs. 2-6.

1886 *Palaeoniscus reticulatus* Williams, pp. 82, 83, fig. 1a, e.

1891 *Palaeoniscus devonicus* Clarke : Woodward, p. 485.

1891 *Palaeoniscus reticulatus* Williams : Woodward, p. 485.

1918 *Rhadinichthys devonicus* (Clarke) = *Rhadinichthys reticulatus* (Williams) : Hussakof & Bryant, p. 182, pls. 59-61, pl. 63, figs. 1, 2, pl. 65, text-figs. 60, 61.

1926 *Rhadinichthys devonicus* (Clarke) : Woodward & White, p. 570.

- 1932 *Palaeoniscus devonicus* Clarke : Woodward, p. 117.  
 1933a *Rhadinichthys devonicus* (Clarke) : Gross, p. 59.  
 1933b *Rhadinichthys devonicus* (Clarke) : Gross, p. 71.  
 1937 *Rhadinichthys devonicus* (Clarke) : Aldinger, p. 204 (name only).  
 1953 *Rhadinichthys devonicus* (Clarke) : Gross, p. 85 (name only).  
 1958 "*Rhadinichthys devonicus*" (Clarke) : Lehman, p. 2136 (name only).  
 1958 "*Rhadinichthys reticulatus*" (Williams) : Lehman, p. 2136 (name only).

DIAGNOSIS (emended). A species reaching a length of 13 cm. Trunk fusiform, elongated ; teeth little larger than those in type species. Bases of teeth on maxilla fused to surrounding bone. Posterior margins of joints of some lepidotrichia delicately denticulated [as in *Elonichthys robisoni* (Hibbert)]. See also Clarke, 1855 : 20, 41 and Hussakof & Bryant, 1918 : 182.

HOLOTYPE. Isolated bones and scales at one time in the Buffalo Museum, from Portage, Ohio and Genesee Shales, New York State.

MATERIAL. Specimens from the British Museum (Natural History). About ten specimens, consisting mainly of scales were examined.

REMARKS. Woodward (1932 : 117) considered *Palaeoniscus devonicus* Clarke to be very similar to *Stegotrachelus finlayi* Woodward & White, but later Gross (1933, 1942), after a comparison of their scales, came to the conclusion that *Rhadinichthys devonicus* (Clarke) should be placed in the genus *Moythomasia*. This is further borne out by a comparison of the text-figures and plates of *Rhadinichthys devonicus* (Clarke) given in Hussakof & Bryant (1918) and the illustrations of *Moythomasia nitida* Gross given in Gross (1953, pl. 4). The maxillae of these two species are very similar, both having the same general proportions and both possessing a slight concavity in their dorsal margins. This maxilla is not at all like that described in *Stegotrachelus finlayi* Woodward & White (Text-fig. 12). The opercular of *Rhadinichthys devonicus* (Clarke) also bears a close resemblance to that seen in *Moythomasia nitida* Gross and finally both the scales and the skull roofing bones are similarly ornamented in the two species. Thus I feel there is every justification for placing *Palaeoniscus devonicus* Clarke (1885) in the genus *Moythomasia*.

### *Moythomasia antiqua* (Williams)

- 1886 *Palaeoniscus antiquus* Williams, pp. 82, 84, fig. 11a, d.  
 1891 *Palaeoniscus antiquus* Williams : Woodward, p. 485.  
 1918 *Rhadinichthys antiquus* (Williams) Hussakof & Bryant, p. 186, pl. 63, fig. 3, pl. 64, text-fig. 62.  
 1933b *Rhadinichthys antiquus* (Williams) : Gross, p. 72.  
 1953 *Rhadinichthys antiquus* (Williams) : Gross, p. 85 (name only).  
 1958 "*Rhadinichthys antiquus*" (Williams) : Lehman, p. 2136 (name only).

DIAGNOSIS. See Williams, 1866 : 82, 84, figs. 2a, d.

HOLOTYPE. Isolated scales, at one time in the Buffalo Museum, from the Portage Group, Sturgeon Point, Erie County, New York.

REMARKS. This species is known only from isolated scales, but as Gross (1933*b*, 1953) has pointed out, they bear a close resemblance to *Moythomasia laevigata* Gross. Although I am loth to accept species based only on scales, for the sake of completeness of the record, I think that they are sufficiently different from the scales of *Moythomasia devonica* (Clarke) and from any of the other species of *Moythomasia* described by Gross (1933*a*, 1933*b*, 1953) to warrant a separate species for their reception.

Family **TEGEOLEPIDAE** Romer, 1945 : 579 (name only)

DIAGNOSIS. Trunk elongated, body cylindrical, skull pointed anteriorly. Fins, apart from caudal, without fulcra, delicate and many rayed. Caudal fin strongly heterocercal, pectoral fin-rays unarticulated, but distally bifurcated. Branchiostegal rays numerous, teeth acutely conical and arranged in two series—an inner row of well spaced, large lanianries and an outer row of numerous, small, closely arranged teeth. Scales where present, rhomboidal, small, narrow and very thin.

REMARKS. I have used this family to include the Upper Devonian genus *Tegeolepis*, but the Triassic genus *Apateolepis* Woodward from the Hawkesbury Beds of New South Wales also appears to be a late relic of this family.

The Tegeolepidae occupy an intermediate position between the Palaeonisciformes on the one hand and the Chondrosteiformes on the other (see remarks on *Tegeolepis clarki*).

Genus **TEGEOLEPIS** Miller, 1892

1888 *Actinophorus* Newberry, p. 179.

DIAGNOSIS (emended). Trunk elongated; body cylindrical, skull pointed anteriorly. Fins, apart from caudal, without fulcra, delicate and many rayed; caudal fin deeply cleft, pectoral fin-rays unarticulated but distally bifurcated. Skull with strongly developed rostrum, postrostral very long and rostro-premaxillo-antorbital without teeth. Maxilla well developed and subopercular of normal palaeoniscoid proportions. Suprascapular very large and extrascapular series composed of four or more bones. Lateral skull wall with well developed infraorbito-supraorbital bone, and dermopterotic extending a considerable distance behind parietals. Gulars numerous, teeth consisting of well-formed, conical lanianries and numerous smaller teeth; scales rhomboidal, small, narrow and very thin; scale covering complete.

TYPE SPECIES. *Actinophorus clarki* Newberry.

REMARKS. This genus was first described by Newberry (1888) under the name *Actinophorus*, but as Miller (1892) pointed out, this genus was already preoccupied by a coleopteran (Creutzer, 1799), and he therefore proposed the new name *Tegeolepis*. Only one species has so far been described.

*Tegeolepis clarki* (Newberry)

(Pls. I, 2 ; Text-fig. 13)

- 1888 *Actinophorus clarki* Newberry, p. 179.  
1890 *Actinophorus clarki* Newberry : Newberry, p. 175, pl. 49, figs. 1, 1a.  
1891 *Actinophorus clarki* Newberry : Woodward, p. 487.  
1892 *Tegeolepis clarki* (Newberry) Miller, p. 717.  
1953 *Tegeolepis clarkii* (Newberry) : Gross, p. 85 (name only).

DIAGNOSIS. A large species reaching almost a metre in length, cranial roof bones and cheek bones ornamented with tubercles and short ridges of enamel.

HOLOTYPE. Fish showing underside of head and pectoral fins, A.M.N.H., No. 230 from the Cleveland Shale, Brooklyn, Cuyahoga County, Ohio (Upper Devonian).

MATERIAL. Specimens from the British Museum (Natural History), latex peels of the holotype and of a second specimen in the American Museum of Natural History, New York. Four specimens were examined.

REMARKS. This species shows many similarities to members of the Chondrosteiformes. The scales are very thin and small in *Tegeolepis clarki* and in this show a condition which could easily lead to the rudimentary scaling found in the later Chondrosteiformes. The pectoral fin devoid of fulcral scales and without articulations in *T. clarki* is again reminiscent of the condition seen in *Chondrosteus* Egerton from the Lias. The pointed snout and well developed rostrum is of the right order to derive not only *Chondrosteus* but even *Palaeopsephurus* MacAlpin. On the other hand, *T. clarki* still has a well developed maxilla of normal palaeoniscoid proportions and a small subopercular. Reduction in the maxilla and enlargement of the subopercular would be necessary before a condition such as that seen in *Chondrosteus* could be achieved. However I have little doubt that the Tegeolepidae were the palaeoniscoid family from which the much later Chondrosteiformes evolved although *Tegeolepis clarki* may not have been the direct ancestor.

DESCRIPTION. *The skull.* The external bones of the skull are delicately ornamented with tubercles and ridges of enamel. On the skull roofing bones the ridges are more pronounced and run along the length of the bones. On the maxilla, infraorbitals, lower jaw and branchiostegal rays the ridges of enamel are finer and not so prominent, intercalating and anastomosing. Superimposed on these ridges are numerous tubercles (see Pl. 2).

The skull of *Tegeolepis clarki* is long with an oblique suspensorium and the orbit situated well forward. The skull roofing bones are only visible on one specimen, A.M.N.H., No. 361, where they have been considerably displaced. The suprascapular is very long (Text-fig. 13), far longer than what is normal in the Palaeonisciformes. In this respect it is very similar to that seen in *Chondrosteus acipenseroides* Egerton, *Chondrosteus hindenburgi* Pompeckj and *Birgeria groenlandica* Stensiö. The extrascapular series appears to be made up of at least four bones (cf. *Acipenser sturio* L.), a pair of small central members, which anteriorly meet the two parietals and two larger bones, one on either side of this median pair which laterally join the dermopterotics.



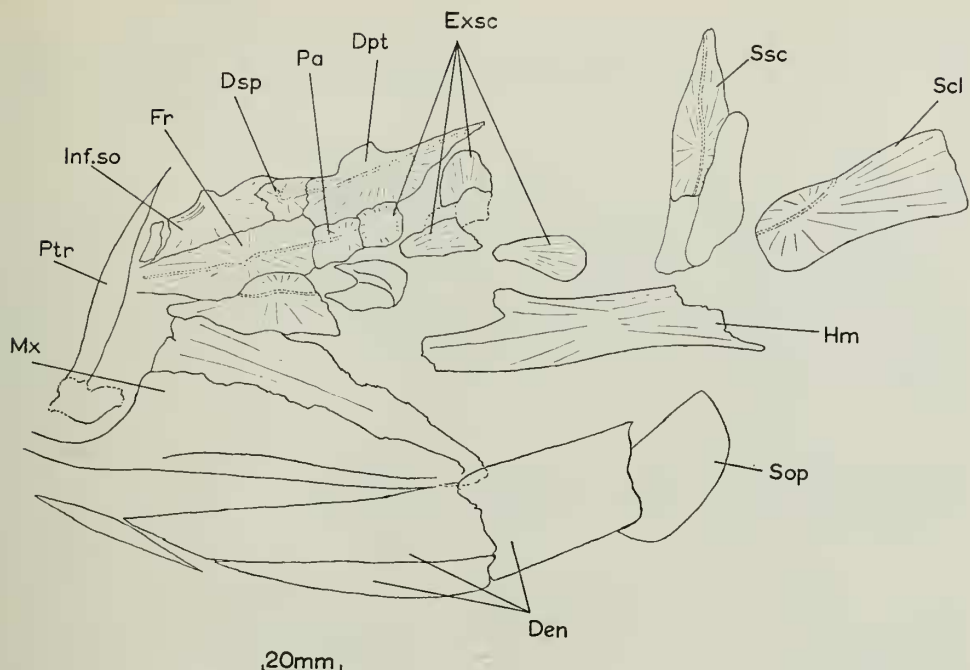


FIG. 13. *Tegeolepis clarki* (Newberry). Sketch of the skull bones on specimen A.M.N.H. 361.

The parietals are small and square in outline and are preceded by a single pair of long frontals. Anteriorly the frontals join the long postrostral. The postrostral from what I can deduce is a single bone which is responsible for the long pointed extension to the head. Anteriorly it is strongly elbowed much as in *Elonichthys serratus* Traquair (Moy-Thomas & Dyne, 1938 : 22). Ventrally the postrostral meets the paired rostro-premaxillo-antorbital. The rostro-premaxillo-antorbital does not bear teeth and can be seen on A.M.N.H. No. 230 (the holotype) anterior to the limits of the lower jaw.

The lateral wall of the skull roof is composed of three bones, the dermopterotic, dermosphenotic and the infraorbito-supraorbital (A.M.N.H., No. 361). The dermopterotic like the suprascapular is a long bone extending posteriorly beyond the limit of the extrascapular series. Anteriorly it makes contact with the frontal and the dermosphenotic, laterally it bounds the extrascapulars and the parietal. The dermopterotic both in shape and position is very similar to that seen in a specimen of *Chondrosteus hindenburgi* Pompeckj (Hennig, 1925) in the Tübingen Museum, and to *Birgeria groenlandica* Stensiö (Nielsen, 1949). Anterior to the dermopterotic is a small dermosphenotic which anteriorly again joins the infraorbito-supraorbital. The infraorbito-supraorbital is much larger than the dermosphenotic and forms part of the dorsal border of the orbit.

The maxilla is of the normal palaeniscoid shape, except that its expanded

posterior position is not as high as in most Palaeonisciformes (B.M.N.H., P.45312, Pl. 2). The posterior expanded portion is gently rounded dorsally and the ventral edge of the maxilla turns slightly upwards anteriorly. The maxilla bears a series of stout conical laniaries, interspersed with a series of much smaller, more numerous teeth. The subopercular is not enlarged (Text-fig. 13) as in *Chondrosteus acipenseroides* Egerton but whether a large opercular existed could not be ascertained. The branchiostegal rays numbered thirty or more members.

Of the remaining skull bones little could be made out, but there is some evidence of an infraorbital series bounding the orbit below and behind.

*The Palate.* The palatoquadrate portion of Meckel's cartilage was ossified and its anterior portion can be seen on A.M.N.H., No. 230. The palatoquadrate is also ossified in *Chondrosteus hindenburgi* (see specimen in Tübingen Museum).

The hyomandibular is both wide and relatively straight, and from its position in A.M.N.H., No. 361 the suspensorium must have been very oblique. The hyomandibular bears a distinct opercular process so that I conclude that a large opercular was probably present. The size, shape and position of the hyomandibular is very reminiscent of the condition seen in the Recent *Polydon*.

*Lower jaw.* The outer surface of the lower jaw is composed of three bones (see B.M.N.H., P.45312). The posterior margin is made up of a stout angular which is preceded antero-dorsally by the surangular. The remainder of the outer surface is made up of the dentary. The disposition of the bones in the lower jaw is very similar to that seen in *Birgeria groenlandica* Stensiö (Nielsen, 1949).

*The paired fins and their girdles.* The supracleithrum is large and broad and can be seen displaced in A.M.N.H., No. 361. The cleithrum was not recognisable on any of the specimens.

The pectoral fin has from sixty-five to seventy rays, the first six of which are the stoutest and the sixth, seventh and eighth the longest. The rays are smooth, distally bifurcated and unarticulated (see B.M.N.H., P.9402).

No specimen shows the pelvic fin but in B.M.N.H., P.9402 (Pl. 1, Pv) part of the endoskeleton of the fin is preserved. The pelvic plate of each fin is slightly concave towards the midline while its lateral border is slightly convex. Posteriorly the plate is expanded and presumably a series of radials were supported at this point. An ossified pelvic plate has been described in *Birgeria mougeoti* Agassiz (Stensiö, 1921 : 192) from the Trias.

*The unpaired fins.* The anal fin, although not present on any of the specimens I have examined, was mentioned by Newberry (1880 : 179) as being small and triangular in outline. However, on B.M.N.H., P.9402 two of the supporting axonosts of the anal fin are visible. These axonosts (Ax) are long and expanded ventrally, and are similar in size and shape to those seen in *Chondrosteus acipenseroides*. The caudal is strongly heterocercal, the dorsal fin unknown.

*Squamation.* The scales are quadrangular, very small and narrow, thin and delicate.

REMARKS. Returning to the Middle Devonian of Europe, in particular the Middle Old Red Sandstone of Scotland, very abundant remains of the palaeoniscoid

*Cheirolepis trailli* Agassiz have been found. In order to elucidate the problem of the homologies of the snout bones in the actinopterygians (treated in the discussion) this material of *Cheirolepis trailli* was re-examined.

Family **CHEIROLEPIDAE** Pander, 1860 : 69

DIAGNOSIS (emended). Trunk elongated, mandibular suspension oblique. Fins of moderate size and composed of numerous delicate rays, closely articulated and branching distally ; fulcral scales prominent. Pelvic fins with extended base line, dorsal fin scarcely longer than deep, and fin elongated. Anal fin arising anterior to dorsal. Caudal fin heterocercal, inequilobate and only slightly forked. Scales minute, thick, covered with enamel and with an internal boss. Scales not overlapping.

REMARKS. This family includes one genus only, *Cheirolepis*, from the Middle Devonian of Europe and the Upper Devonian of North America. The affinities of this family remain obscure, no later palaeoniscoid family appears to have been derived from it.

Genus **CHEIROLEPIS** Agassiz, 1835

DIAGNOSIS. See Woodward, 1891 : 451.

TYPE SPECIES. *Cheirolepis trailli* Agassiz.

***Cheirolepis trailli*** Agassiz

(Text-fig. 14)

- 1828 " Second Gamrie Ichthyolite " Pentland, p. 364.
- 1835 *Cheirolepis traillii* Agassiz, **2**, 1, p. 130, pl. i.d, pl. i.e, fig. 4.
- 1835 *Cheirolepis uragus* Agassiz, **2**, 1, p. 132, pl. i.e, figs. 1-3.
- 1844 *Cheirolepis cummingiae* Agassiz, **2**, 1, p. 301 (name only).
- 1844 *Cheirolepis cummingiae* Agassiz, p. 45, pl. 12.
- 1848 *Cheirolepis velox* M'Coy, p. 302.
- 1848 *Cheirolepis curtus* M'Coy, p. 302.
- 1848 *Cheirolepis macrocephalus* M'Coy, p. 303.
- 1855 *Cheirolepis curtus* M'Coy : M'Coy, p. 580, pl. 2d, fig. 1.
- 1855 *Cheirolepis macrocephalus* M'Coy : M'Coy, p. 580, pl. 2d, fig. 3.
- 1855 *Cheirolepis traillii* Agassiz : M'Coy, p. 581.
- 1855 *Cheirolepis uragus* Agassiz : M'Coy, p. 581.
- 1855 *Cheirolepis velox* M'Coy : M'Coy, p. 581, pl. 2d, fig. 2.
- 1855 *Cheirolepis uragus* Agassiz : Eichwald, **1**, 2, p. 1575, pl. 57, fig. 21.
- 1860 *Cheirolepis cummingiae* Agassiz : Pander, pl. 8, figs. 1-3, 5.
- 1860 *Cheirolepis trailli* Agassiz : Pander, pl. 8, fig. 4.
- 1860 *Cheirolepis curtus* M'Coy = *Cheirolepis cummingiae* Agassiz : Egerton, p. 123.
- 1860 *Cheirolepis macrocephalus* M'Coy = *Cheirolepis trailli* Agassiz : Egerton, p. 123.
- 1860 *Cheirolepis velox* M'Coy : Egerton, p. 123.
- 1867 *Cheirolepis trailli* Agassiz : Powrie, p. 152.
- 1867 *Cheirolepis cummingiae* Agassiz : Powrie, p. 152.
- 1867 *Cheirolepis velox* M'Coy = *Cheirolepis cummingiae* Agassiz : Powrie, p. 152.

- 1867 *Cheirolepis uragus* Agassiz : Powrie, p. 152.  
 1875a *Cheirolepis cummingiae* Agassiz : Traquair, p. 240, pl. 17.  
 1888 *Cheirolepis trailli* Agassiz : Traquair, p. 517.  
 1890a *Cheirolepis trailli* Agassiz : Traquair, p. 485.  
 1891 *Cheirolepis trailli* Agassiz : Woodward, p. 452.  
 1895 *Cheirolepis trailli* Agassiz : Traquair, p. 250, pl. 3, fig. 4.  
 1907 *Cheirolepis* sp., Goodrich, p. 768, pl. 45, fig. 13.  
 1909 *Cheirolepis* sp., Goodrich, p. 310, text-fig. 288.  
 1925 *Cheirolepis trailli* Agassiz : Watson, p. 816, text-figs. 1-3.  
 1925 *Cheirolepis cummingii* Agassiz : Jaekel, p. 418, text-fig. 10.  
 1927 *Cheirolepis cummingii* Agassiz : Jaekel, p. 931, text-fig. 58.  
 1935 *Cheirolepis trailli* Agassiz : Watson, p. 166, fig. 36.  
 1937 *Cheirolepis trailli* Agassiz : Aldinger, p. 196, text-figs. 50, 51.  
 1947 *Cheirolepis trailli* Agassiz : Gross, pp. 139, 156, text-figs. 24, 27.  
 1947 *Cheirolepis trailli* Agassiz : Lehman, p. 8, pls. 5, 6.  
 1953 *Cheirolepis trailli* Agassiz : Gross, p. 108, text-fig. 10 a, b.

DIAGNOSIS. See Woodward, 1891 : 452 and Watson, 1925 : 816-821, 824.

SYNTYPES. Imperfect fishes ; olim T. S. Traill Collection. Part of the Traill Collection was subsequently deposited in the Bootle Museum, however this did not contain any material of *Cheirolepis* and since it seems probable that it is no longer in existence I propose as the neotype specimen B.M.N.H., 49182, in counterpart, from the Middle Old Red Sandstone, Lethen Bar, Nairnshire, Scotland.

MATERIAL. Specimens from the British Museum (Natural History), the Royal Scottish Museum, the University Museum Cambridge, University College London, the Geological Survey and Museum and D. M. S. Watson's collection. Approximately eighty specimens were examined.

REMARKS. Although *Cheirolepis trailli* has been adequately described there are two points concerning its structure which have aroused much discussion. First, the opercular apparatus with the two bones "X" and "Y" lying between the opercular and the preopercular. The bone "Y" of Watson (1925 : 819) is clearly the dermohyal whilst the bone "X" of Watson (1925 : 819) is undoubtedly an accessory opercular (for a full discussion of this see earlier under *Watsonichthys pectinatus*). Secondly, the snout region ; according to Watson (1925, text-figs 1-3) there are already at this early stage in actinopterygian evolution three distinct pairs of bones making up the snout, the premaxilla, antorbital and rostral. Westoll (1937c : 570) doubts this but does not give any reason for so doing. I have re-examined the snout region of *Cheirolepis trailli* and this is included in the following description. On re-examining the snout region I have come across a very nice specimen of *Cheirolepis trailli* in the Zoology Museum, Cambridge, which shows the skull roof in dorsal view. Since this skull roof differs in one or two important points from the description given by Watson (1925 : 816) it too is included in the following description.

DESCRIPTION. *The skull.* Several specimens including U.M.Z.C. 425 show a different arrangement of the roofing bones from that described by Watson (1925). Anterior to the dermopterotic is a large bone which considerably extends the lateral margin of the skull roof. This bone I have termed the dermosphenotic-infraorbito-



supraorbital (Text-fig. 14). However it would appear that within this genus this bone is a variable character and may either be present as a single ossification (Dsp.Inf.so in Text-fig. 14) or as two independent ossifications (I.tem. and Pt.f, Watson, 1925, text-fig. 1).

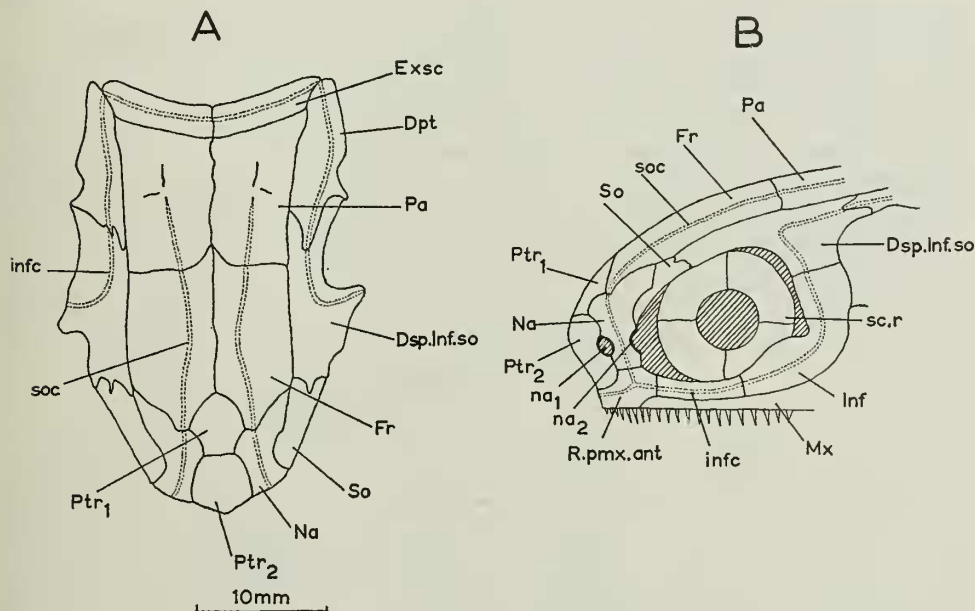


FIG. 14. *Cheirolepis trailli* Agassiz. (a) Reconstruction of skull roof. Mainly from U.M.Z.C. 425. (b) Reconstruction of snout.

The snout region is never very satisfactorily preserved and consequently the interpretation of it is open to question, also there appears to be some variability in the bone arrangement from specimen to specimen. My own interpretation of the snout region is given in Text-fig. 14B, and I believe that there is a single paired ossification ventro-anteriorly, the rostro-premaxillo-antorbital. Evidence of this ossification and of the nasal which lies above it can be seen on B.M.N.H., P.4345 and also on B.M.N.H., 35778 and P.6421. The nasal (B.M.N.H., P.4345) bears two notches, one anteriorly for the anterior nostril (na<sub>1</sub>) and the other posteriorly for the posterior nostril (na<sub>2</sub>). Dorso-posteriorly the nasal joins the supraorbital.

Thus on my interpretation the snout of *Cheirolepis trailli* is very similar to that seen in other primitive palaeoniscoids, in particular *Stegotrachelus finlayi* and *Tegeolepis clarki*. Further, since it seems probable that the primitive actinopterygian snout was composed basically of three bones only, the paired nasals, the paired rostro-premaxillo-antorbitals and a median postrostral (see later under discussion), *Cheirolepis trailli* now fits into place and is no longer an exception to the rule. As a further justification for my reconstruction of the snout region of *Cheirolepis trailli*, I would like to point out that I have not seen an independent rostral element below the parasemionotid level of organization.



*Cheirolepis canadensis* Whiteaves

(Text-fig. 15)

1881 *Cheirolepis canadensis* Whiteaves, p. 33.1889 *Cheirolepis canadensis* Whiteaves : Whiteaves, p. 90, pl. 8.1891 *Cheirolepis canadensis* Whiteaves : Woodward, p. 457.1918 *Cheirolepis canadensis* Whiteaves : Hussakof & Bryant, p. 181, pl. 7 vii, figs. 1, 2.1947 *Cheirolepis canadensis* Whiteaves : Gross, pp. 139, 156, text-figs. 25b, 26, 28.1947 *Cheirolepis canadensis* Whiteaves : Lehman, pp. 1-44.1953 *Cheirolepis canadensis* Whiteaves : Gross, pp. 85, 108, text-fig. 10c.

DIAGNOSIS. See Woodward, 1891 : 457 and Lehman, 1947 : 1.

HOLOTYPE. Imperfect fish ; Geological Survey of Canada, Ottawa, from Scaumenac Bay, P.Q., Canada (Upper Devonian).

MATERIAL. Specimens from the British Museum (Natural History).

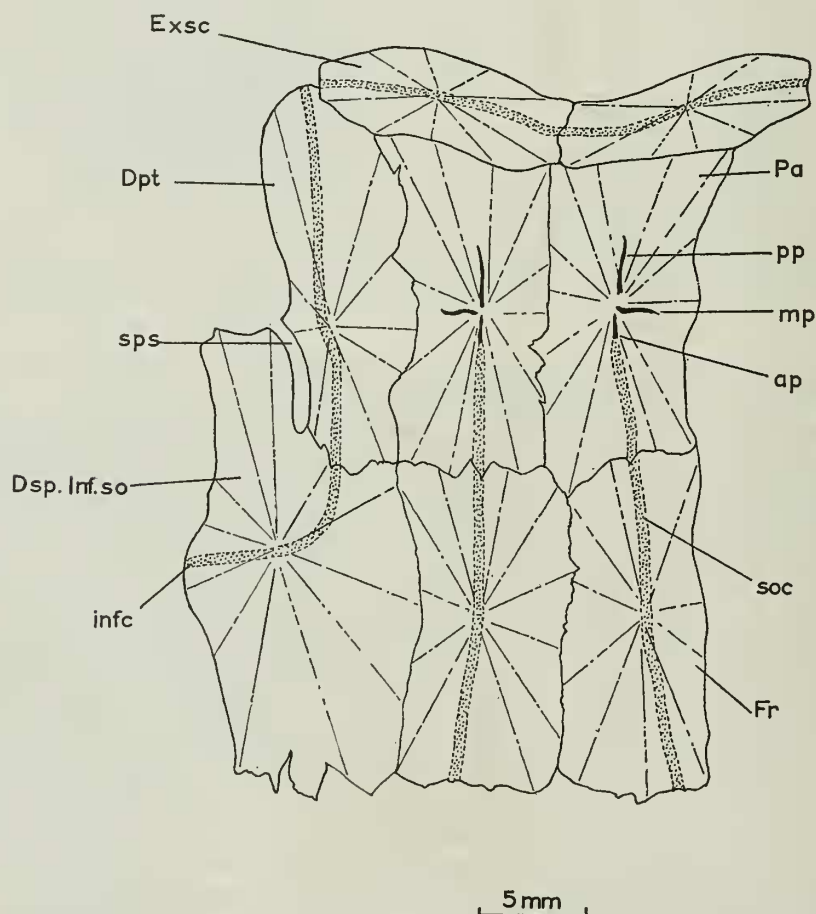


FIG. 15. *Cheirolepis canadensis* Whiteaves. Reconstruction of skull roof. From B.M.N.H., P.6815.

REMARKS. Although this species has been fairly adequately described, the skull roof has not so far been very clearly figured. One specimen, B.M.N.H., P.6815, shows a perfectly preserved skull roof in dorsal view and in order to supplement that description already given for *Cheirolepis trailli* it is described below.

DESCRIPTION. *The skull roof.* The dermal bones of the skull roof and the course of the sensory canals, as far as can be determined, are shown in Text-fig. 15. The parietals and frontals are rectangular and of approximately the same size. The dermopterotic is large and a little longer than the parietal. Anteriorly the dermopterotic joins the very large dermosphenotic-infraorbito-supraorbital. This is a similar ossification to that already described in *Cheirolepis trailli*. One point of difference, however, is that in *Cheirolepis canadensis* it is produced posteriorly to a greater extent and between this posterior projection of the dermosphenotic-infraorbito-supraorbital and the dermopterotic there is a well marked slip (sps). This slit represents the spiracular notch and a similar slit in an almost identical position has been described in *Kentuckia deani* (Eastman) by Rayner (1951 : 57).

### III. DISCUSSION

#### *The snout region in actinopterygians*

The sensory canals in actinopterygians influence the ontogeny of the dermal bones through which they pass (Pehrson, 1922, 1940, 1944a, b). Basically one bone primordium develops in relation to each sensory canal neuromast, thus a series of bone primordia is formed along the length of each sensory canal. The number of bone primordia varies with the number of neuromasts which go to make up any one canal. Thus the number of neuromasts must have been large in acanthodians (Stensiö, 1947, text-fig. 11, B, C) but small in palaeoniscoids, subholosteans and holosteans. Normally these bone primordia fuse together to give the adult sensory canal carrying bones. The adult sensory canal bones then are usually formed from two or more bone primordia which belong to one and the same series. It has been argued by Stensiö (1947) that some sensory canal carrying bones also include, besides the sensory canal elements, anamestic components. The term anamestic was first introduced by Westoll (1937a) and has been used by Stensiö (1947) for the non-sensory line bearing elements of the head in fishes and amphibians. In evidence Stensiö (1947 : 125) quotes such forms as *Amia*, *Acipenser* and teleosts, where he believes that the median dorsal series of anamestic bones have entered into the formation of the frontals and parietals of both sides. In contrast most modern embryologists believe that adult sensory canal bones in both fishes and amphibians are composed exclusively of bone elements developed in relation to sensory canals. Stensiö further believes, and I agree with him entirely, that in certain cases adjoining elements from sensory lines may fuse together, particularly if one of the sensory lines fails to differentiate ; only by this view can the presence of binary bone primordia in relation to certain sensory lines in *Amia* be explained. In other cases Stensiö (1947) believes that sensory lines or parts of them persist even though the underlying bone originally connected with them has disappeared, for example, the anterior division of the supramaxillary line in *Amia* and teleosts.

Finally, Stensiö (1947), in contradistinction to Pehrson (1922, 1940, 1944a, b) and Westoll (1937b, 1940, 1944) believes that the sensory line grooves and pit lines in bony fishes play fundamentally the same part in the embryonic formation of sensory line bones as do the sensory canals proper, and Lekander's later work (1949) on the sensory line system of the Ostariophysi would tend to support Stensiö. Stensiö's case for this point of view is entirely convincing and logical. Thus we see that the dermal bones of the head of bony fishes are referable to two categories, sensory line elements and anamestic elements. The sensory line carrying bones may be formed entirely from sensory line elements or from both sensory line elements and anamestic elements which have fused. The anamestic bones, or "space fillers" as Westoll (1937a) considered them, are a primitive constituent of the dermal skeleton of the head and are, in my opinion, of equal phyletic importance to the sensory canal bones.

From an examination of palaeoniscoids, subholosteans and holosteans it cannot be doubted that in these groups an almost complete series of bones is found in connection with the sensory line canals, grooves and pit lines of the head; further, these sensory canals, grooves and pit lines took an active part in the embryological formation of the associated series of dermal bones and retained their connection with them. In discussing the snout region in actinopterygians it is possible to trace the fates of different dermal bones because of their fixed relationship to the contained sensory canals and to one another.

For some time now the terminology used for the bones in the snout region of palaeoniscoids, subholosteans, holosteans and teleosts has become more and more confused. As a result the rather awkward nomenclature applied to these snout bones has grown up. This nomenclature has been discussed at length by both Nielsen (1942) and Westoll (1944), but without really clarifying the situation. Since many of the palaeoniscoids described in this paper show the snout region particularly well, a reassessment of the situation can usefully be given.

The primitive actinopterygian snout was composed of three bones only, the paired nasals, the paired rostro-premaxillo-antorbitals and the single postrostral. This condition can be seen in some Devonian genera such as *Tegeolepis clarki*, *Cheirolepis trailli* (Text-fig. 14) and *Stegotrachelus finlayi* (Text-fig. 12) and is quite common among Carboniferous genera (i.e. *Canobius elegantulus* Text-fig. 16 A, *Rhadinichthys canobiensis* (16B), *Kentuckia deani* (16D), *Paramesolepis tuberculata* (16E), *Pyritocephalus sculptus* (16G), *Haplolepis tuberculata* (16H)). This condition is still retained by much later palaeoniscoids and subholosteans, as for example *Palaeoniscus freieslebeni*, Text-fig. 16C, from the Upper Permian and *Diaphorognathus gillioti*, Text-fig. 16F, from the Lower Triassic.

Of the three original bones comprising the snout, two are paired, sensory canal bearing elements and the third a single anamestic bone. This single bone occupying a position anterior to the frontals and lying along the midline of the skull is termed the postrostral. The postrostral never carries a branch of the sensory canal system and is normally bounded on either side by the nasals. Frequently, though not invariably (see later under movement of nares), the postrostral forms the lateral

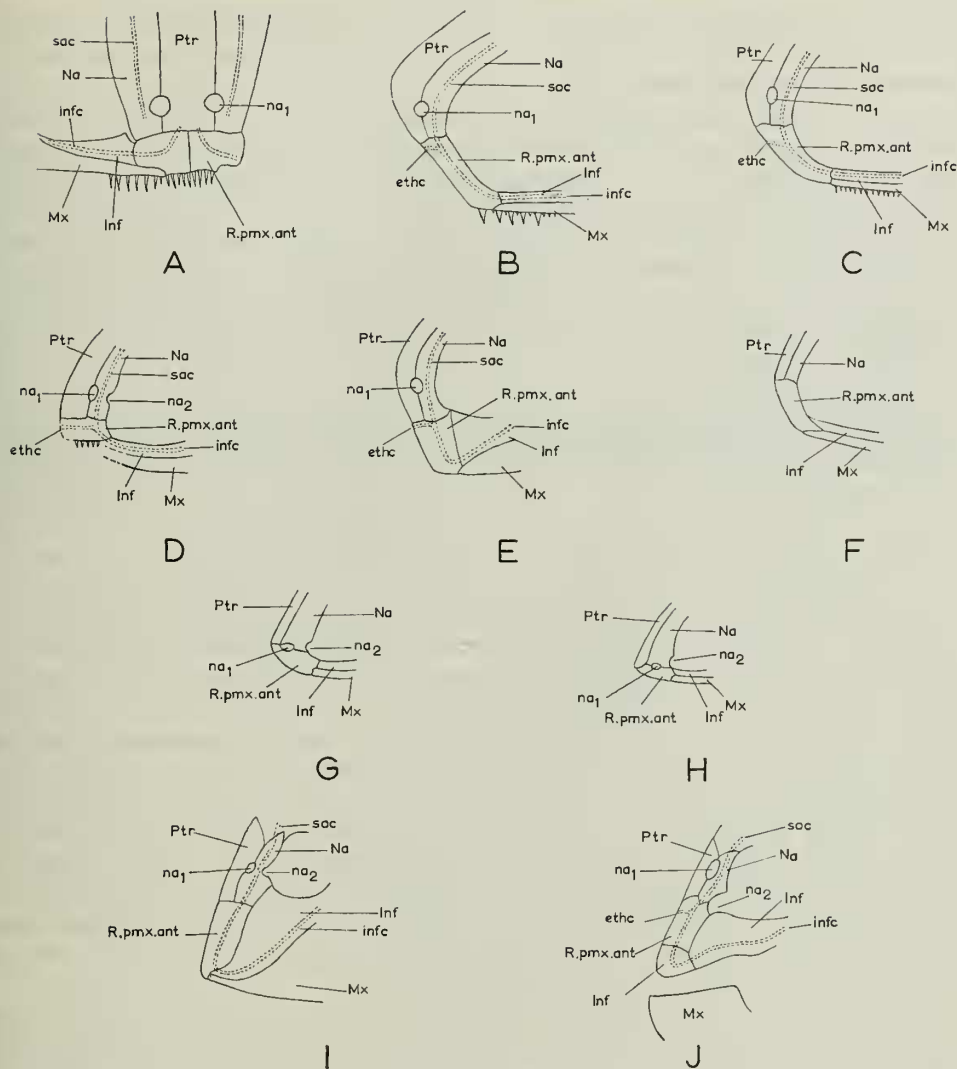


FIG. 16. A. *Canobius elegantulus* Traquair. Lower Carboniferous. After Moy-Thomas & Dyne, 1938. B. *Rhadinichthys canobiensis* Traquair. Lower Carboniferous. After Moy-Thomas & Dyne, 1938. C. *Palaeoniscus freislebeni* Blainville. Upper Permian. After Westoll in Aldinger, 1937. D. *Kentuckia deani* (Eastman). Lower Carboniferous. After Rayner, 1951. E. *Paramesolepis tuberculata* (Traquair). Lower Carboniferous. After Moy-Thomas & Dyne, 1938. F. *Diaphorognathus gillioti* (Priem). Lower Triassic. After Brough, 1933. G. *Pyritocephalus sculptus* Fritsch. Upper Carboniferous. After Westoll, 1944. H. *Haplolepis tuberculata* (Newberry). Upper Carboniferous. After Westoll, 1944. I. *Platysomus superbus* Traquair. Lower Carboniferous. After Moy-Thomas & Dyne, 1938. J. *Bobasatrania mahavavica* White. Lower Triassic. After Lehman, 1957.



boundary of the anterior nostril ( $na_1$ ). The two paired bones of the primitive actinopterygian snout as already mentioned are the nasals and the rostro-premaxillo-antorbital respectively.

The two nasals primitively lie one on either side of the postrostral and are sensory canal bearing elements. The anterior portion of the supraorbital sensory canal passes completely along their length. Most authors use the term nasal when referring to this pair of bones, and since they are intimately associated with the nostrils the terminology is sound and should not give rise to any confusion. Each nasal primitively bears two distinct notches, one for the anterior (in the anterior margin) and the other for the posterior (in the posterior margin) nostril. In subsequent evolution the position of these nostrils alters and one or both of these notches may be lost.

The two rostro-premaxillo-antorbitals lie anterior to the postrostral and nasals and meet in the midline (Text-fig. 16A). The rostro-premaxillo-antorbital primitively contains a three branched part of the infraorbital canal. The infraorbital canal passes forwards from the first infraorbital into the posterior part of the rostro-premaxillo-antorbital. This canal continues from its point of entry to the centre of the bone where it divides into two branches, one of which runs nearly parallel with the postero-dorsal margin and anastomoses with the anterior end of the supraorbital canal at the point where the nasal bone meets the rostro-premaxillo-antorbital. The other of the two branches into which the infraorbital canal divides extends forward as the ethmoid commissure. Thus the sensory canal system in this bone often looks "Y" shaped (Text-fig. 16B, C, D, E, J). I have used the rather cumbersome term rostro-premaxillo-antorbital since by subsequent fragmentation this bone gives rise to the rostral, the antorbital and the premaxilla. For the same bone Moy-Thomas & Dyne (1938) and Rayner (1951) have used the term rostral, while Westoll (1944) has used both dentigerous rostral and pre-maxilla. Nielsen (1942), however, has used a very similar terminology to mine, calling the bone rostro-antorbital-premaxillary. I feel justified in using the term rostro-premaxillo-antorbital rather than Nielsen's (1942) term because by far the most common initial fragmentation of this bone is into two separate bones, the rostro-premaxillary and the antorbital (Text-fig. 18).

The rostro-premaxillo-antorbital primitively bears teeth along its ventral edge as can be seen in *Stegotrachelus finlayi* (Text-fig. 12) and *Cheirolepis trilli* (Text-fig. 14) from the Devonian and in *Canobius elegantulus* (Text-fig. 16A), *Rhadinichthys canobiensis* (Text-fig. 16B) and *Kentuckia deani* (Text-fig. 16D), all from the Lower Carboniferous. Let us now examine the fate of the rostro-premaxillo-antorbital. Fragmentation of this bone has occurred independently in different groups of palaeoniscoids to give at least three different bone patterns. By far the most common pattern was for the rostro-premaxillo-antorbital first to fragment into two separate bones, the rostro-premaxillary and the antorbital. One of the earliest palaeoniscoids to show this fragmentation is *Moythomasia nitida* (Text-fig. 18G) from the Devonian, whilst several of the Lower Carboniferous forms I have described in this paper show a similar pattern (*Cosmoptychius striatus* (Text-fig. 18C), *Watsonichthys pectinatus*



(Text-fig. 18D), *Nematoptychius greenocki* (Text-fig. 18F)). This pattern is still retained in much later forms such as *Lawnia taylorensis* (Text-fig. 18H) from the Permian and *Pteronisculus arambourgi* (Text-fig. 18A) and *Birgeria groenlandica* (Text-fig. 18B) from the Lower Triassic. The rostro-premaxillary in all these examples bears teeth and contains the ethmoid commissure, while the antorbital which lies posterior to it still retains the characteristic "Y" shaped division of the infraorbital sensory canal system. In the antorbital the anteriorly directed branch of the infraorbital canal extends forwards passing through the rostral process and then into the rostro-premaxillary as the ethmoid commissure (see p. 280). The antorbital may or may not bear teeth ventrally, depending upon where the fragmentation occurred. Thus the antorbital bears teeth in such forms as *Cosmoptychius striatus* (Text-fig. 18C), *Watsonichthys pectinatus* (Text-fig. 18D) and *Mesonichthys aitkeni* (Text-fig. 18E), while teeth are not present on the antorbital of *Pteronisculus arambourgi* (Text-fig. 18A), *Birgeria groenlandica* (Text-fig. 18B), *Nematoptychius greenocki* (Text-fig. 18F), *Moythomasia nitida* (Text-fig. 18G) and *Lawnia taylorensis* (Text-fig. 18H).

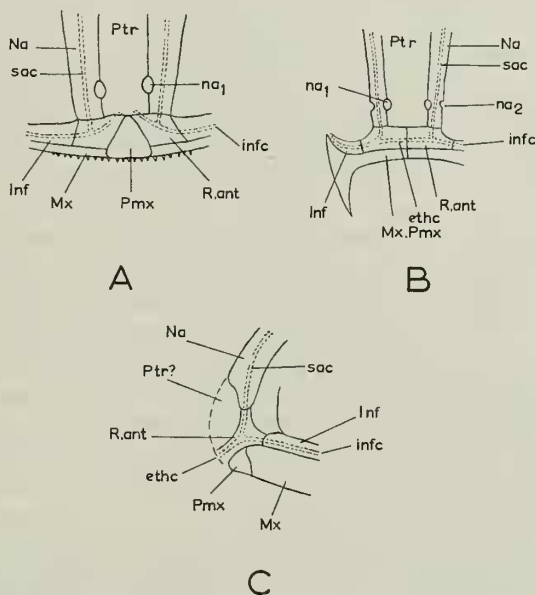


FIG. 17. A. *Canobius ramsayi* Traquair. Lower Carboniferous. After Moy-Thomas & Dyne, 1938. B. *Cornuboniscus budensis* White. Upper Carboniferous. After White, 1939. C. *Cleithrolepis granulata* Egerton. Triassic. After Wade, 1935.

Different but much more uncommon methods of fragmentation of the rostro-premaxillo-antorbital are shown in Text-fig. 17. In *Canobius ramsayi* (Text-fig. 17A), for example, a large central element is present, the toothed premaxilla, while the remainder of the bone from which it fragmented represents the rostro-antorbital and contains the ethmoid commissure. It seems likely that in this case

after the initial fragmentation the two premaxillae have fused to give this single median structure. In *Cleithrolepis granulata* (Text-fig. 17C), fragmentation has resulted in paired premaxillae and a rostro-antorbital again with the contained ethmoid commissure. The condition seen in *Cornuboniscus budensis* (Text-fig. 17B) is more difficult to explain, there being two possible alternatives, either the rostro-premaxillo-antorbital has split into a rostro-antorbital and a paired premaxilla with the latter fusing with the anterior ends of the maxillae of either side, which is the view I favour, or the rostro-premaxillo-antorbital has not fragmented and has thus retained its ancestral condition with the maxillae of either side extending anteriorly to meet in the midline beneath it.

Returning to the more common type of fragmentation—that of the rostro-premaxillo-antorbital into rostro-premaxillary and antorbital, it would seem that this is the ancestral condition from which the later holosteans and teleosts were derived. Going one step further, it appears more likely that the holostean condition was derived from forms which possessed a rostro-premaxillary and a toothless antorbital (i.e. those forms where the antorbital does not take part in the upper jaw margin, viz. *Pteronisculus arambourgi* (Text-fig. 18A), *Birgeria groenlandica* (Text-fig. 18B), *Lawnia taylorensis* (Text-fig. 18H), *Nematoptychius greenocki* (Text-fig. 18F), *Moynthomasia nitida* (Text-fig. 18G)) rather than from those forms in which the antorbital bears teeth (i.e. those forms where the antorbital takes part in the formation of the upper jaw margin, viz. *Cosmoptychius striatus* (Text-fig. 18C), *Watsonichthys pectinatus* (Text-fig. 18D), *Mesonichthys aitkeni* (Text-fig. 18E)).

From forms possessing a paired toothed rostro-premaxillary and an antorbital which does not enter into the formation of the upper jaw margin the next step is for the rostro-premaxillary to fragment to give a separate rostral, containing the ethmoid commissure, and a toothed premaxilla (this is in fact the holostean condition, see Text-fig. 19). In *Watsonulus eugnathoides* (Lower Triassic) Text-fig. 19A, this step has not yet occurred and thus in the snout there is still a rostro-premaxillary and an antorbital present, but in other members of the same family, also from the Lower Triassic, fragmentation of the rostro-premaxillary has taken place giving a separate rostral and a premaxilla, the rostral containing the ethmoid commissure (viz. *Parasemionotus labordei* (Text-fig. 19B)). Thus in the pholidophoroid-teleost line this final fragmentation into a separate premaxilla and rostral did not occur until the Lower Triassic (if one believes that the parasemionotids were ancestral to the pholidophoroids, Gardiner, 1960), and similarly in the amioid line (Text-fig. 19G, H, I) since the amioids were undoubtedly also derived from the parasemionotids. In the separate semionotoid line, however, fragmentation of the rostro-premaxillary into rostral and premaxilla had occurred by the Upper Permian as shown by *Acentrophorus varians* (Text-fig. 19J).

At about the same time as this final fragmentation into rostral and premaxilla was taking place the median postrostral bone underwent reduction and was finally lost. The postrostral is not present in the parasemionotids or in the two lines which lead from them, the pholidophoroids and the amioids; it was presumably reduced and lost prior to the parasemionotid grade of organization. However,

the postrostral is still present in the early members of the semionotid line, viz. *Acentrophorus varians* (Text-fig. 19J), *Semionotus capensis* (Gardiner, 1960, text-fig. 71). Correlated with the loss of the postrostral are fundamental changes in the position of the nostrils, which will be dealt with later in the discussion.

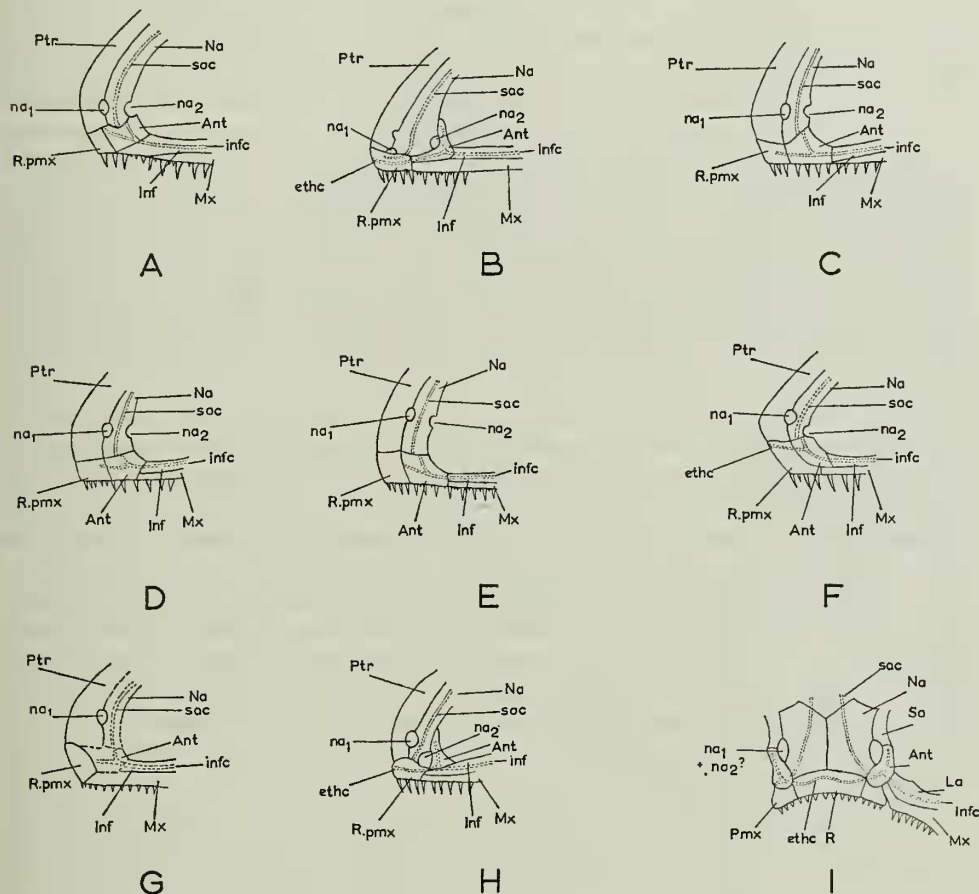


FIG. 18. A. *Pteronisculus arambourgi* Lehman. Lower Triassic. After Lehman, 1952. B. *Birgeria groenlandica* Stensiö. Lower Triassic. After Nielsen, 1949. C. *Cosmoptychius striatus* (Agassiz). Lower Carboniferous. D. *Watsonichthys pectinatus* (Traquair). Lower Carboniferous. E. *Mesonichthys aikenii* n. gen. (Traquair). Upper Carboniferous. F. *Nematoptychius greenocki* (Traquair). Lower Carboniferous. G. *Moythomasia nitida* Gross. Upper Devonian. After Gross, 1955. H. *Lawnia taylorensis* Wilson. Permian. After Wilson, 1953. I. *Ichthyokentema purbeckensis* (Davis). Upper Jurassic. After Griffith & Patterson, 1963.

Summing up, then, as a result of this fragmentation of the palaeoniscoid rostro-premaxillo-antorbital and the reduction and subsequent loss of the postrostral, the snout region of the holostean composed of basically four pairs of bones, the nasals,

rostrals, premaxillae and antorbitals was derived. However, in almost all holosteans and teleosts the rostral is a single bone in the adult condition. Nevertheless, Pehrson (1940) is of the opinion that in *Amia* this single bone represents the numerous separate rostral bones of primitive forms. In *Lepisosteus* the rostral arises as a paired bone in relation to the ethmoid commissure (De Beer, 1937 : 114). Thus it would seem that the rostral was originally paired, as indeed it must have been if we postulate its derivation from the paired rostro-premaxillo-antorbital of primitive forms. That some fusion of the original paired bones of the snout has occurred can be seen in *Birgeria groenlandica* Stensiö from the Lower Triassic where the rostro-premaxilla is a single median bone (formed by the fusion of the originally paired rostro-premaxillaries). Further, in some of the parasemionotids this would also appear to be the case. From such a median single rostro-premaxillary in a parasemionotid the condition described by Griffith and Patterson (1963) in the pholidophoroid *Ichthyokentema purbeckensis* (Davis) (Text-fig. 18I) from the Upper Jurassic could have been derived by the splitting off of two premaxillae to leave a median toothed rostral (for further discussion on this point see Griffith and Patterson, 1963).

Let us now follow the fate of these bones in the teleosts. The nasals are not easily confused, lying as they do anterior to the frontals and always containing the anterior portion of the supraorbital sensory canal. The nasals do, however, show considerable reduction in some groups. The rostral bone only persists as a recognisable bone in a few primitive teleosts ; thus in the Recent *Elops saurus* it is represented by four small components through which the ethmoid commissure runs (Text-fig. 19D). In *Ctenothrissa* from the Cenomanian (Text-fig. 19E), a fish which in grade of organization stands between the Elopidae and the more advanced acanthopterygians (Patterson, 1963), the rostral (dermethmoid of many authors) is a small plate of dermal bone intimately associated with the underlying mesethmoid, and the ethmoid commissure no longer passes through this bone but must have run above it. The rostral is finally unrecognizable in the more advanced acanthopterygians and in other advanced teleosts.

The premaxilla, which is still small in *Pholidophorus* from the Triassic, becomes much enlarged in the later teleosts, while the antorbital becomes reduced and lost. The antorbital is still present in some primitive teleosts such as *Elops saurus* (Text-fig. 19D) and see Gosline (1961 : 22) for a few others, while Patterson (1963) has given a good evolutionary series showing its reduction and loss within the acanthopterygians. *Ctenothrissa radians* (Text-fig. 19E) from the Cenomanian still retains a moderate-sized antorbital but in *Hoplopteryx sinus*, again from the Cenomanian and a member of the Trachichthyidae, it is represented by a very small element (the infraorbital sensory canal no longer piercing it even) and this is the last appearance of the antorbital in the acanthopterygians. However, some Recent members of the family Holocentridae, which is a family close to the Trachichthyidae, still possess an antorbital. At the same time that the antorbital was being reduced there was an increase in size of the first infraorbital in the teleosts. The first infraorbital (the most anterior infraorbital) is that bone which in the primitive palaeoniscoid

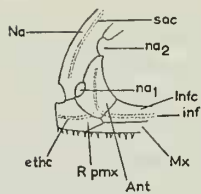


lies immediately behind the rostro-premaxillo-antorbital, above the maxilla and through which the infraorbital canal passes. In the teleost this same bone is normally referred to as the lachrymal. I would favour the retention of this dual nomenclature, calling this bone the first infraorbital in anything below the teleost grade of organization, and lachrymal in the teleost. Since the antorbital is usually wanting in teleosts it would be as well to define the exact position of the lachrymal. In teleosts and pholidophoroids the lachrymal always articulates with the edge of the lateral ethmoid, its ventral edge lies lateral to the maxilla but not necessarily touching it, and the palatine articulates with its inner surface.

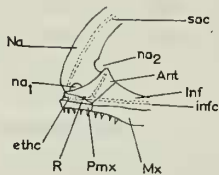
Having examined the homologies of the different bones that go to make up the actinopterygian snout, the more difficult problem of the position of the nostrils may be examined. No one, apart from Saint-Seine (1949 : 292), appears to have discussed or even mentioned this basic and important question. The primitive palaeoniscoid ancestors possessed two pairs of nostrils, the anterior nostril ( $na_1$ ) lying between the postrostral and the anterior edge of the nasal, and the posterior nostril ( $na_2$ ) lying in the posterior edge of the nasal, these two nostrils then being separated by the nasal bone and with the contained branch of the supraorbital sensory canal passing between them (Text-fig. 16D, I, J ; see also Recent *Acipenser* Text-fig. 20A). It seems probable that in many of the reconstructions (Text-fig. 16A, B, C, E, F) the rather more insignificant posterior nostril has been omitted by the different authors, since it is often only represented by the smallest of notches. In all these primitive palaeoniscoids (Text-fig. 16) the infraorbital canal anastomoses with the supraorbital sensory canal at the junction between the nasal and the rostro-premaxillo-antorbital. With the initial fragmentation of the rostro-premaxillo-antorbital into rostro-premaxillary and antorbital this anastomosis between the infraorbital and supraorbital sensory canal is broken, the dorsally directed branch of the infraorbital canal in the antorbital reaching the dorsal margin of the antorbital posteriorly to the point where the supraorbital canal reaches the ventral margin of the nasal (Text-fig. 18). In subsequent evolution towards the holostean-teleost condition the shape of the antorbital has changed, it has become produced dorsally until that portion containing the dorsal extension of the infraorbital sensory canal has come to lie posterior to the nasal and at the same time to form the posterior margin of the posterior nostril (Text-figs. 18B, H ; 19C, D, I).

In order to arrive at the condition seen in both holosteans and teleosts, with regard to the nostrils, it is necessary to get both of the nostrils to the lateral side of the supraorbital sensory canal. The problem is not an easy one and to postulate the migration of the anterior nostril appears to me to be the only solution. There are certain palaeoniscoids which show how this migration may have occurred. For example, in *Birgeria groenlandica* (Text-fig. 20B), the anterior nostril ( $na_1$ ) lies right at the antero-ventral extremity of the nasal bone. Again, in *Haplolepis tuberculata* (Text-fig. 20C) the anterior nostril lies midway along the ventral edge of the nasal. The real difficulty would seem to be for the anterior nostril to cross the supraorbital sensory canal, however the anastomosis between the supraorbital and infraorbital sensory canals has been broken, so that migration of the anterior

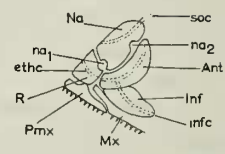




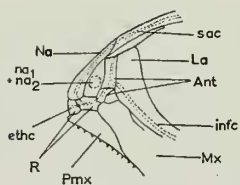
A



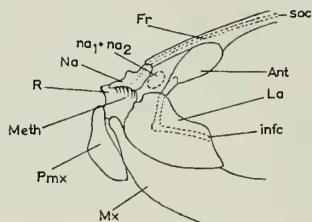
B



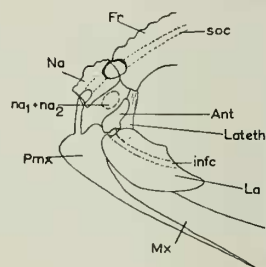
C



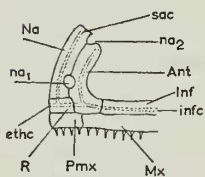
D



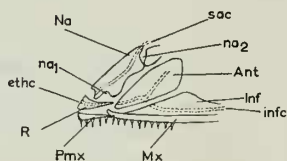
E



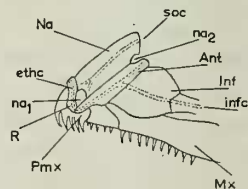
F



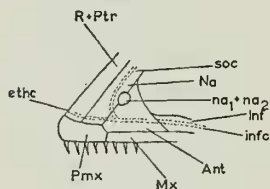
G



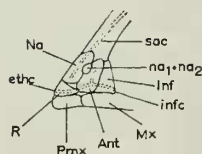
H



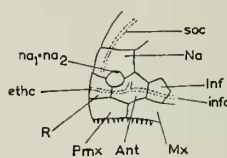
I



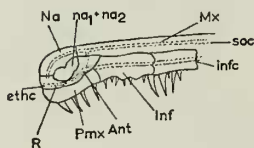
J



K



L



M

nostril down and round the ventral limits of the nasal is now possible. A further clue to this complex problem is given by a study of the Recent *Polypterus senegalus* (Text-fig. 20D) in which the anterior nostril is confluent with the posterior nostril, with the anterior portion of the nasal bone and its contained supraorbital sensory canal partially separating them. It would seem that in *Polypterus senegalus* we have the answer to the problem, that is that the anterior nostril migrated round the anterior edge of the nasal, passing round the contained supraorbital sensory canal to end up on the posterior side of the nasal. The migration of the anterior nostril can be correlated with the reduction and subsequent loss of the postrostral, which primitively formed the anterior boundary of this nostril.

Let us now examine some of the later actinopterygians to trace the subsequent fate of this anterior nostril. In the Parasemionotidae the anterior nostril has already migrated to the lateral nasal margin, so that the nasal now has two separate notches in its lateral border for the anterior and posterior nostrils respectively (Text-fig. 19A, B). In the more advanced Pholidophoridae (Text-fig. 19C) the two nostrils are still quite separate but in the later teleosts further upward migration of the anterior nostril has taken place until both the anterior and posterior nostrils have become confluent and the teleost condition is one in which normally only one nostril (however still clearly divided internally) is to be seen.

In the Amioidea, which were derived from the same ancestral stock as the Pholidophoroidea (Gardiner, 1960) both nostrils are present, both lying lateral to the supraorbital sensory canal (Text-fig. 19G, H, I).

In the Semionotoidea, however, only one nostril is present (Text-fig. 19J, K, L, M), and this single aperture represents the fusion of the anterior with the posterior nostril<sup>1</sup>. Already in the Permian *Acentrophorus* (Text-fig. 19J), this fusion had occurred and this lends further weight to the argument that the Semionotoidea and Amioidea had quite separate ancestries (Gardiner, 1960).

Unfortunately the condition of the nostrils in the Pycnodontoidea is not at all clear, but in both the Platysomidae (Text-fig. 16I) and the Amphicentridae (and from one or other of these two groups the pycnodonts must have been derived), and also the later Bobasatraniaidae (Text-fig. 16J), the snout is of the primitive palaeoniscoid condition with the nostrils still one on either side of the supraorbital sensory canal.

In the Aspidorhynchoidea the condition is similar to that in the teleosts in that the two nostrils have become confluent.

FIG. 19. A. *Watsonulus eugnathoides* Piveteau. Lower Triassic. After Lehman, 1952. B. *Parasemionotus labordei* Lehman. Lower Triassic. After Lehman, 1952. C. *Pholidophorus similis* Woodward. Kimeridgian. After Saint-Seine, 1949. D. *Elops saurus* Linnaeus. Recent. E. *Ctenothrissa radians* (Agassiz). Cenomanian. After Patterson, 1963. F. *Hoplopteryx sinus* Woodward. Cenomanian-Turonian. After Patterson, 1963. G. *Paracentrophorus madagascariensis* Piveteau. Lower Triassic. After Gardiner, 1960. H. *Caturus drieri* Thiollère. Kimeridgian. After Saint-Seine, 1949. I. *Amia calva* Linnaeus. Recent. J. *Acentrophorus varians* (Kirkby). Upper Permian. After Gardiner, 1960. K. *Lepidotes semiserratus* Agassiz. Upper Lias. L. *Dapedium politum* Leach. Lower Lias. M. *Lepisosteus osseus* Linnaeus. Recent.

<sup>1</sup> In some specimens of *Lepisosteus* the two nostrils may be separated by a narrow bridge of bone.

Finally, anastomosis of the infraorbital sensory canal with the supraorbital canal can take place at a later stage if the two components lie close enough together. This has occurred in the Recent *Polypterus senegalus* (Text-fig. 20D) and in the Recent *Lepisosteus osseus* (Text-fig. 19M), while a similar condition is observable in *Paracentrophorus madagascariensis* (Text-fig. 19G) from the Lower Triassic.

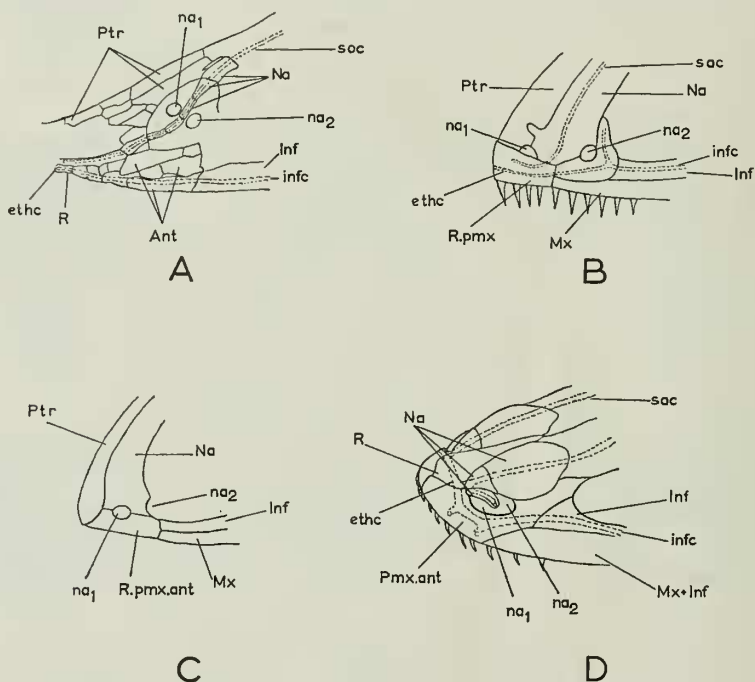


FIG. 20. A. *Acipenser sturio* Linnaeus. Recent. B. *Birgeria groenlandica* Stensiö. Lower Triassic. After Nielsen, 1949. C. *Haplolepis tuberculata* (Newberry). Upper Carboniferous. After Westoll, 1944. D. *Polypterus senegalus* Cuvier. Recent. Partly after Jarvik, 1942.

#### IV. SUMMARY

This paper is intended as a clearing of the ground for a revision of the palaeoniscoid fauna of the British Carboniferous. The type species of four genera from this fauna are redescribed, and for comparative purposes members of four Devonian and two Permian genera are redescribed.

Three new palaeonisciform families are erected. They are the Cosmoptychiidae, closely allied to the Acrolepidae of Aldinger (1937); the Rhabdolepidae, a family fairly close to the Elonichthyidae of Aldinger (1937), and the Stegotrachelidae. The family Tegeolepidae is shown to be intermediate in structure between the Palaeonisciformes and the Chondrosteiformes. A new genus *Mesonichthys* is erected for *Elonichthys aitkeni* Traquair (1886), and a new species, *R. saarbrueckensis*, is added to the genus *Rhabdolepis* Troschel (1857).

The homologies of the bones of the actinopterygian snout are discussed, and it is shown that the primitive actinopterygian snout was composed of three bones only, the paired nasals, the paired rostro-premaxillary-antorbital and the median postrostral. Subsequent fragmentation of the rostro-premaxillary-antorbital has occurred independently in different groups of palaeoniscoids to give at least three different bone patterns. The most common pattern was for the rostro-premaxillary-antorbital to split into two bones, the rostro-premaxillary and the antorbital, and this type of snout appears to have been present in the ancestors of the holosteans and teleosts. Changes in the position of the nostrils during actinopterygian evolution are also discussed, and it is suggested that the condition in teleosts has been reached by migration of the anterior nostril round the ventral edge of the nasal, this migration following breakage of the anastomosis between the infra- and supra-orbital sensory canals, and being correlated with loss of the postrostral.

#### V. ACKNOWLEDGMENTS

I wish to thank Dr. E. I. White, F.R.S., of the British Museum (Natural History), and Dr. C. D. Waterston, of the Royal Scottish Museum, for the opportunity of studying the collections which form the basis of this work ; Dr. C. Patterson for much fruitful discussion, and Mr. H. A. Toombs for his generous help.

#### VI. REFERENCES

- AGASSIZ, L. 1833-44. *Recherches sur les Poissons fossiles*. 5 vols. 1420 pp., 396 pls. with supplement. Neuchâtel. [For dates of publication of various sections of text and plates see Woodward & Sherborn (1890).]
- 1844-45. *Monographie des Poissons fossiles du Vieux Grès Rouge ou Système Dévonien (Old Red Sandstone) des Îles Britanniques et de Russie*. xxxvi + 171 pp., 43 pls. Neuchâtel.
- AITKEN, J. 1874. Notes on the discovery of a new fish of the genus *Acrolepis*, Ag., in the Millstone Grit, near Hebden Bridge, Yorkshire. *Trans. Manchr. Geol. Soc.*, **13** : 36-43.
- ALDINGER, H. 1937. Permische Ganoidfische aus Ostgrönland. *Medd. Grönland*, Kjøbenhavn, **102**, 3 : xliv + 392 pp., 44 pls.
- BERGH, L. S. 1940. Classification of Fishes, both Recent and Fossil. *Trav. Inst. zool. Acad. Sci. URSS*, Moscow, **5**, 2 : 1-517 pp., 190 figs.
- BOLTON, H. 1895. The animal life of the Lancashire Coal Measures. *Trans. Manchr. micr. Soc.*, **1895** : 1-13, pl. 3.
- BRONN, H. G. 1829. Ueber die Fisch-Abdrücke in Eisenstein-Nieren des Mittel-Rheinischen Steinkohlen — Gebirges, und über *Palaeoniscum macropterum* n. sp. insbesondere. *Z. Minerv.*, Frankfurt, **2** : 483.
- CASIER, E. 1952. Contributions à l'étude des Poissons fossiles de la Belgique, X. Un Palaeoniscoïde du Famennien inférieur de la Fagne : *Stereolepis marginis* n. gen., n. sp. *Bull. Inst. Sci. nat. Belg.*, Bruxelles, **28**, 47 : 1-17, pls. 1, 2.
- 1954. Contributions à l'étude des Poissons fossiles de la Belgique, XI. Note additionnelle relative à "*Stereolepis*" (= *Osorioichthys* nov. nom.) et à l'origine de l'interoperculaire. *Bull. Inst. Sci. nat. Belg.*, Bruxelles, **30**, 2 : 1-12, 3 figs.
- CLARKE, E. 1885. On the Higher Devonian fauna of Ontario County, New York. *Bull. U.S. Geol. Surv.*, Washington, **3**, 16 : 39-120, pls. 1-3.
- DE BEER, G. R. 1937. *The development of the vertebrate skull*. xxiii + 552 pp., 143 pls. Oxford.
- DEMANET, F. 1941. Faune et stratigraphie de l'étage namurien de la Belgique. *Mém. Mus. Hist. nat. Belg.*, Bruxelles, **97** : 156-283.

- DORSMAN, L. 1945. The marine fauna of the Carboniferous in the Netherlands. *Med. geol. Bur. ned. Mijnggeb.*, Heerlen (C) **4**, 3, 3 : 77.
- EGERTON, P. 1860. Palicthyologic Notes. No. 12. Remarks on the Nomenclature of the Devonian Fishes. *Quart. J. Geol. Soc. Lond.*, **16** : 119-136, 7 figs.
- EICHWALD, E. 1852-1868. *Lethaea Rossica, ou Paléontologie de la Russie*, **1**. *L'ancienne période etc.* (1860). Atlas 59 pls. (1855). Stuttgart.
- GARDINER, B. G. 1960. A revision of certain Actinopterygian and Coelacanth fishes, chiefly from the Lower Lias. *Bull. Brit. Mus. (Nat. Hist.) Geol.*, London, **4** : 239-384, pls. 36-43.
- 1962. *Namaichthys schroederi* Gürich and other palaeozoic fishes from South Africa. *Palaeontology Lond.*, **5** : 9-21, pl. 6.
- GOLDENBERG, C. F. 1873. *Fauna Saraepontana fossilis*. — *Die fossilen Thiere aus der Steinkohlenformation von Saarbrücken*, **1**. 26 pp., 2 pls. Saarbrücken.
- GOLDFUSS, G. A. 1847. *Beiträge zur vorweltlichen Fauna des Steinkohlengebirges*. 26 pp., 5 pls. Bonn.
- GOODRICH, E. S. 1907. On the scales of fishes, living and extinct, and their importance in classification. *Proc. Zool. Soc. Lond.*, **1907** : 751-774.
- 1909. In LANKESTER, R. *A Treatise on Zoology, IX. Vertebrate Craniata (First Fascicle : Cyclostomes and Fishes)*. xvi + 518 pp., 515 figs.
- GOSLINE, W. A. 1961. Some osteological features of modern lower teleostean fishes. *Smithson. misc. Coll.*, Washington, **142**, 3 : 1-42, 8 figs.
- GRIFFITH, J. & PATTERSON, C. 1963. The structure and relationships of the Jurassic fish *Ichthyokentema purbeckensis*. *Bull. Brit. Mus. (Nat. Hist.) Geol.*, London, **8** : 1-43, pls. 1-4.
- GROSS, W. 1933a. Die Fische des baltischen Devons. *Palaeontographica*, Stuttgart, **79**, A : 1-74, pls. 1-6.
- 1933b. Die Wirbeltiere des rheinischen Devons. *Abh. preuss. geol. Landesanst.*, Berlin (N.F.) **154** : 5-84, pls. 1-11.
- 1942. Die Fischfauna des baltischen Devons und ihre biostratigraphische Bedeutung. *KorrespBl. NaturfVer. Riga*, **64** : 373-436, 19 figs.
- 1953. Devonische Palaeonisciden-Reste in Mittel und Osteuropa. *Paläont. Z.*, Berlin, **27** : 85-112, pls. 4-7.
- HEIDE, S. v. d. 1943. Le faune ichthyologique du Carbonifère supérieur des Pays-Bas. *Meded. geol. Sticht. Maastricht* (C) **4**, 3, 2 : 1-65, pls. 1-4.
- 1955. In JONGMANS, W. J. & HEIDE, S. v. d. Flore et faune du Carbonifère inférieur de l'Égypte. *Meded. geol. Sticht.*, s'Gravenhage (n.s.) **8** : 73-75, pl. 17.
- HENNIG, E. 1925-26. *Chondrosteus hindenburgi* Pomp., ein Stör des Württemberg. Ölschiefers. *Palaeontographica*, Stuttgart, **67** : 115-134, pl. 9.
- HINDE, G. J. 1879. On Conodonts from the Chazy and Cincinnati Group of the Cambro-Silurian, and from the Hamilton and Genesee-Shale Division of the Devonian, in Canada and the United States. *Quart. J. Geol. Soc. Lond.*, **35** : 351-369, pls. 15-17.
- HUSSAKOF, L. & BRYANT, W. L. 1918. Catalog of the fossil fishes in the Museum of the Buffalo Society of Natural Science. *Bull. Buffalo Soc. nat. Sci.*, **12** : 1-346, pls. 1-70.
- JAEKEL, O. 1925. Das Mundskelett der Wirbeltiere. *Morph. Jb.*, Leipzig, **55** : 402-484.
- 1927. Der Kopf der Wirbeltiere. *Ergebn. Anat. EntwGesch.*, Wiesbaden, **27** : 815-974, 93 figs.
- KELLER, G. 1934. Stratigraphische und paläogeographische untersuchung an der Grenze Namur — Westfal Westdeutschlands und angrenzender Gebiete. IV. Beiträge zur Kenntnis der Fauna und Flora des oberen namurs (Magerkohlschichten). *Abh. preuss. geol. Landesanst.*, Berlin (N.F.) **162** : 46-53.
- LANGENHAN, A. 1905. *Fauna und Flora des Rotliegenden in der Umgebung von Friedrichroda in Thüringen*. 12 pp. Friedrichroda. (Gotha, K. Schwalbe).
- LEHMAN, J. P. 1947. Description des quelques exemplaires de *Cheirolepis canadensis* (Whiteaves). *K. svenska VetenskAkad. Handl.*, Stockholm (3) **24**, 4 : 1-40, pls. 1-9.



- 1958. In GRASSE. *Traité de Zoologie, Anatomie, Systématique, Biologie*, 13, *Agnathes et Poissons* 3 : 1813–2758, figs. 1308–1889. Paris.
- LEKANDER, B. 1949. The sensory line system and the canal bones in the head of some Ostariophysi. *Acta. zool. Stockh.*, **30** : 1–131, 67 figs.
- M'COY, F. 1848. On some new Ichthyolites from the Scotch Old Red Sandstone. *Ann. Mag. Nat. Hist.*, London (2) **2** : 297–312.
- 1855. In SEDGWICK, A. & M'COY, F. *A synopsis of the classification of the British Palaeozoic Rocks by . . . A. Sedgwick. . . With a detailed systematic description of the British Palaeozoic Fossils in the Geological Museum of the University of Cambridge*, by F. M'COY. (Appendix A. Description of a few species from Wales and Westmoreland . . . by J. W. Salter), III : i–xcviii, 407–662, pls. 3 D–K. London & Cambridge.
- MILLER, S. A. 1889–1897. *North American Geology and Paleontology*. 793 pp. Ohio. First Appendix : (1892, pp. 665–718). Second Appendix : (1897, pp. 719–793).
- MOY-THOMAS, J. A. 1939. *Palaeozoic Fishes*. ix + 149 pp., 33 figs. London.
- MOY-THOMAS, J. A. & DYNE, M. B. 1938. Actinopterygian fishes from the Lower Carboniferous of Glencartholm, Eskdale, Dumfriesshire. *Trans. Roy. Soc. Edinb.*, **59** : 437–480, pls. 1, 2.
- MORRIS, J. 1854. *A Catalogue of British Fossils . . . with reference to their geological distribution and to the localities in which they have been found*. vii + 372 pp. London.
- NEWBERRY, J. S. 1888. On the fossil fishes of the Erie Shale of Ohio. *Trans. N.Y. Acad. Sci.*, **7** : 178–180.
- 1890. The Palaeozoic Fishes of North America. *Monogr. U.S. geol. Surv.*, Washington, **16** : 1–340, pls. 1–53.
- NIELSEN, E. 1936. Some few preliminary remarks on Triassic Fishes from East Greenland. *Medd. Grønland*, Kjøbenhavn, **112**, 3 : 1–55, 19 figs.
- 1942. Studies on Triassic fishes from East Greenland. I. *Glaucolepis* and *Boreosomus*. *Medd. Grønland*, Kjøbenhavn, **138** : 1–403 + 31, pls. 1–30.
- NYBELIN, O. 1956. Les canaux sensoriels du museau chez *Elops saurus* (L.). *Ark. Zool.*, Uppsala (2) **10** : 453–458, 3 figs.
- PANDER, C. H. 1860. *Über die Saurodipteryinen, Dendrodonten, Glyptolepiden und Cheirolepiden des Devonischen systems*. ix + 89 pp., 17 pls. St. Petersburg.
- PATERSON, R. 1837. On the fossil organic remains found in the coal formation at Wardie near Newhaven. *J. Edinb. New. Phil.*, **23** : 146–155.
- PATTERSON, C. 1963. A review of Mesozoic Acanthopterygian Fishes with special reference to those of the English Chalk. *Philos. Trans.*, London (B). In press.
- PEACH, C. W. 1872. Additions to the list of Fossils and Localities of the Carboniferous Formation in and around Edinburgh. *Brit. Ass. Trans.*, London, **1871** : 109.
- PEHRSON, T. 1922. Some points in the cranial development of teleostomian fishes. *Acta zool. Stockh.*, **3** : 1–63, 24 figs.
- 1940. The Development of the Dermal Bones in the Skull of *Amia calva*. *Acta zool. Stockh.*, **21** : 1–50, 50 figs.
- 1944a. Some Observations on the Development and Morphology of the Dermal Bones in the Skull of *Acipenser* and *Polydon*. *Acta zool. Stockh.*, **25** : 27–48, 11 figs.
- 1944b. The Development of the Latero-sensory Canal Bones in the Skull of *Esox lucius*. *Acta zool. Stockh.*, **25** : 135–157, 17 figs.
- PENTLAND, C. 1828. In MURCHISON, R. I. Supplementary Remarks on the Strata of the Oolitic Series, and the Rocks associated with them, in the Counties of Sutherland and Ross, and in the Hebrides. *Trans. Geol. Soc. Lond.* (2) **2** : 353–368.
- POHLIG, H. 1892. Altpermische Saurierfährten, Fische und Medusen der Gegend von Friedrichroda in Thür. In TASCHENBERG, E. O. W. and others. *Festschrift zum Siebenzigsten Geburtstage R. Leuckarts. Dem verehrten Jubilar dargebracht von seinen dankbaren Schülern, etc.* xv + 413 pp., 40 pls. Leipzig.

- POWRIE, J. 1867. On the Genus *Cheirolepis*, from the Old Red Sandstone. *Geol. Mag., Lond.* (1) **4** : 147-152, 2 figs.
- PRUVOST, P. 1919. La Faune Continentale du Terrain Houiller du Nord de la France. *Mém. Carte géol. dét. Fr.*, Paris : 404.
- 1930. La Faune Continentale du Terrain de la Belgique. *Mém. Mus. Hist. nat. Belg.*, Bruxelles, **44** : 113-141.
- RAYNER, D. H. 1951. On the cranial structure of an early palaeoniscid *Kentuckia* gen. nov. *Trans. Roy. Soc. Edinb.*, **62** : 53-83, 12 figs.
- ROGERS, I. 1907. On fossil fish. *Rept. Devon Ass. Adv. Sci.*, Plymouth, **39** : 394-398.
- ROMER, A. S. 1945. *Vertebrate Paleontology*. 2nd ed., ix + 687 pp., 377 figs. Chicago.
- SAINT-SEINE, P. 1949. Les poissons des Calcaires Lithographiques de Cerin. *N. Arch. Mus. Hist. nat. Lyon*, **2** : vii + 357 + 27 pp., 26 pls.
- SAUVAGE, H. E. 1888. Poissons du terrain Houiller de Commentry. In FAYOL, M. and others. *Études sur le terrain Houiller de Commentry*, **3**, 1(b) : 39-120, pls. 1-16. St. Étienne.
- 1890. Bassin Houiller et Permien d'Autun et d'Epinac, 3. Poissons Fossiles. *Étud. Gîtes min. Fr.*, Paris, **1890** : 1-31, pls. 1-5.
- STENSIÖ, E. A. 1921. *Triassic Fishes from Spitzbergen, Part 1*. 307 pp., 35 pls. Vienna.
- 1947. The sensory lines and dermal bones of the cheek in fishes and amphibians. *K. svenska Vetensk. Akad. Handl.*, Stockholm (3) **24**, 3 : 1-195, 38 figs.
- SUSTA, V. 1932. Predbezna zprava o nalezu supix a zulu gladkovnich ryle a juie fauny z urstev karvinskych (Vorläufige Bericht über die Schuppen und die Zähne der Süsswasserfische und anderer Fauna aus den Karwiner Schichter). *Sborn. priv. Spolec. Mor.*, Ostrave, **7** : 135-141.
- TRAQUAIR, R. H. 1866. Description of *Pygopterus greenockii* (Agassiz) : with notes on the structural relations of the genera *Amblypterus* and *Eurynotus*. *Proc. Roy. Soc. Edinb.*, **5** : 597-599.
- 1867. Description of *Pygopterus greenockii*, with notes on the structural relations of the genera *Pygopterus*, *Amblypterus* and *Eurynotus*. *Trans. Roy. Soc. Edinb.*, **24** : 701-713, pl. 1.
- 1875. On Some Fossil Fishes from the neighbourhood of Edinburgh. *Ann. Mag. Nat. Hist.*, London (4) **15** : 258-268, pl. 1.
- 1875a. On the structure and systematic position of the genus *Cheirolepis*. *Ann. Mag. Nat. Hist.*, London (4) **15** : 237-249, pl. 1.
- 1876. On New and little known fossil fishes from the Edinburgh district, No. 1. *Proc. Roy. Soc. Edinb.*, **9** : 262-272.
- 1877a. On New and little known fossil fishes from the Edinburgh district, No. 3. *Proc. Roy. Soc. Edinb.*, **9** : 427-445.
- 1877b. On the Agassizian genera *Amblypterus*, *Palaeoniscus*, *Gyrolepis* and *Pygopterus*. *Quart. J. Geol. Soc. Lond.*, **33** : 548-578.
- 1877c. The ganoid fish of the British Carboniferous formations. Part I. *Palaeoniscidae*. *Palaeontogr. Soc. (Monogr.)*, London, **31** : 1-60, pls. 1-7.
- 1879. Fossil fishes from the Edinburghshire and Linlithgowshire Oil Shales. *Proc. R. Phys. Soc. Edinb.*, **5** : 113-128.
- 1882. Notice of new fish remains from the Blackband Ironstone of Borough Lee, near Edinburgh, No. 3. *Geol. Mag. Lond.* (2) **9** : 540-546.
- 1886. New *Palaeoniscidae* from the English Coal Measures. *Geol. Mag. Lond.* (3) **3** : 440-442.
- 1887. Remarks on the Fossils of the Bone Bed at Abden. *Trans. Edinb. Geol. Soc.*, **5** : 314-315.
- 1888. Notes on the nomenclature of the fishes of the Old Red Sandstone of Great Britain. *Geol. Mag. Lond.* (3) **5** : 507-517.
- 1890. List of the fossil Dipnoi and Ganoidei of Fife and the Lothians. *Proc. Roy. Soc. Edinb.*, **17** : 385-400.

- 1890a. On the Fossil Fishes found at Achanarras Quarry Caithness. *Ann. Mag. Nat. Hist.*, London (6) **6** : 479-486.
- 1895. In HARVIE-BROWN, J. A. & BUCKLEY, T. E. *A Vertebrate Fauna of the Moray Basin*, **2** : 235-285, pls. 1-9. Edinburgh.
- 1897. List of the fossil fish remains occurring in the bone bed at Abden, near Kinghorn, Fifeshire. *Proc. Geol. Ass. Lond.*, **15** : 143-145.
- 1901. The ganoid fish of the British Carboniferous formations. Part I. Palaeoniscidae. *Palaeontogr. Soc. (Monogr.)*, London, **31** : 61-87, pls. 8-18.
- 1907. Report on Fossil Fishes collected by the Geological Survey of Scotland from Shales exposed on the shore near Gullane, East Lothian. *Trans. Roy. Soc. Edinb.*, **46** : 103-117, pls. 1, 2.
- 1909. The ganoid fish of the British Carboniferous formations. Part I. Palaeoniscidae. *Palaeontogr. Soc. (Monogr.)*, London, **31** : 107-122, pls. 24-30.
- TROSCHER, F. H. 1857. Beobachtungen über die Fische in den Eisennieren des Saarbrücker Steinkohlengebirges. *Verh. naturh. Ver. preuss. Rheinl.*, Bonn, **14** : 1-19, pls. 1, 2.
- WARD, J. 1890. The Geological features of the North Staffordshire Coalfields, their organic remains, their range and distribution, with a Catalogue of the Fossils of the Carboniferous System of North Staffordshire. *Trans. N. Staffs. Instn Min. Mech. Engrs.*, Newcastle, **10** : iv + 189 pp., 9 pls.
- WATERSTON, C. D. 1954. Catalogue of Type and Figured Specimens of Fossil Fishes and Amphibians in the Royal Scottish Museum, Edinburgh. *Trans. Edinb. Geol. Soc.*, **16** : x + 91 pp.
- WATSON, D. M. S. 1925. The structure of certain Palaeoniscids and the relationships of that group with other bony fish. *Proc. Zool. Soc. Lond.*, **1925** : 815-870.
- 1928. On some points in the structure of Palaeoniscid and other allied fish. *Proc. Zool. Soc. Lond.*, **1928** : 49-70.
- 1935. In WILSON, G. V. and others. The Geology of the Orkneys. *Mem. Geol. Surv. Scotland*, Edinburgh. viii + 205 pp., 8 pls.
- WELBURN, E. D. 1899. Fish fauna of the Lower Coal Measures of the Halifax and Littleborough districts. *Proc. Yorks. Geol. (Polyt.) Soc.*, Leeds, **13** : 419-432, pls. 61, 62.
- WESTOLL, T. S. 1937a. On the cheek bones in Teleostomian fishes. *J. Anat. Lond.*, **71** : 362-382, 8 figs.
- 1937b. On a specimen of *Eusthenopteron* from the Old Red Sandstone of Scotland. *Geol. Mag. Lond.*, **74** : 507-524.
- 1937c. On a remarkable fish from the Lower Permian of Autun, France. *Ann. Mag. Nat. Hist.*, London (10) **19** : 553-578, 7 figs.
- 1940. New Scottish material of *Eusthenopteron*. *Geol. Mag. Lond.*, **77** : 65-73, pl. 2.
- 1944. The Halolepididae, a new family of Late Carboniferous bony fishes. A study in taxonomy and evolution. *Bull. Amer. Mus. Nat. Hist.*, New York, **83** : 1-122, pls. 1-10.
- WHITE, E. I. 1927. The Fish-Fauna of the Cementstones of Foulden, Berwickshire. *Trans. Roy. Soc. Edinb.*, **55** : 255-287, 46 figs.
- 1937. The Fishes of the "Crangopsis Bed" at Ardross, Fifeshire. *Geol. Mag. Lond.*, **74** : 411-428, 17 figs.
- 1939. A New Type of Palaeoniscoid Fish, with Remarks on the Evolution of the Actinopterygian Pectoral Fins. *Proc. Zool. Soc. Lond. (B)* **109** : 41-61, pl. 1.
- WHITEAVES, J. F. 1881. On some remarkable fossil fishes from the Devonian rocks of Scaumenac Bay, P.Q., with descriptions of a new genus and three new species. *Canad. Nat.*, Montreal (n.s.) **10** : 27-35.
- 1889. Illustrations of the fossil fishes of the Devonian rocks of Canada. *Trans. Roy. Soc. Can.*, Ottawa, **6** : 77-96.
- WILLIAMS, H. U. 1886. Notes on the fossil fishes of the Genesee and Portage Black Shales. *Bull. Buffalo Soc. nat. Sci.*, **5** : 81-84.

- WOODWARD, A. S. 1891. *Catalogue of the Fossil Fishes in the British Museum (Natural History)* London, **2**. xliv + 567 pp., 16 pls. Brit. Mus. (Nat. Hist.), London.
- 1932. In ZITTEL, K. A. VON. *Text-Book of Palaeontology*, **2**. [Revised English edition]. xvii + 464 pp., 533 figs. London & New York.
- WOODWARD, A. S. & SHERBORN, C. D. 1890. *A Catalogue of British Fossil Vertebrata*. xxxv + 396 pp. London.
- WOODWARD, A. S. & WHITE, E. I. 1926. The fossil fishes of the Old Red Sandstone of the Shetland Islands. *Trans. Roy. Soc. Edinb.*, **54** : 567-571, pl. 3.

## VII. LETTERING USED IN TEXT-FIGURES

A	anal fin	l	lepidotrichia
Ang	angular	La	lacrimal
Ant	antorbital	Lateth	lateral ethmoid
a.Op	accessory opercular		
ap	anterior pit line	mc	mandibular sensory canal
Ax	axonost	Meth	mesethmoid
		mp	median pit line
Bd	basidorsal	Mx	maxilla
Bo	baseost		
Br	branchiostegal ray	Na	nasal
Bv	basiventral	na <sub>1</sub>	anterior nasal aperture (nostril)
		na <sub>2</sub>	posterior nasal aperture (nostril)
Cl	cleithrum		
Clav	clavicle	Op	opercular
		or	orbit
D	dorsal fin	orp	postmaxillary sensory line
Den	dentary		
Dpt	dermopterotic	Pa	parietal
dr	distal radials	Pcl	postcleithrum
Dsp	dermosphenotic	pi	pineal foramen
Dsp.Inf.so	dermosphenotic-infraorbital-supraorbital	Pmx	premaxilla
		Pmx.ant	premaxillo-antorbital
Dyh	dermohyal	Pop	preopercular
		pp	posterior pit line
ethc	ethmoid commissure	Ptr	postrostral
Exsc	extrascapular	Pv	pelvic plate
Fr	frontal	R	rostral
		r	radial
Gu	gular plate	R.ant	rostro-antorbital
		r.p	rostral process
ha	haemal arch	R.pmx	rostro-premaxillary
hc	supramaxillary sensory line	R.pmx.ant	rostro-premaxillo-antorbital
Hm	hyomandibular		
Hy	hypural	Sbo	suborbital
		ScCor	scapulo-coracoid
Ih	infrahaemal	Scl	supracleithrum
Inf	infraorbital	s.com	supratemporal commissure
infc	infraorbital sensory canal	sc.r	sclerotic ring
Inf.so	infraorbital-supraorbital	Sn	supraneural
Iop	interopercular	So	supraorbital
Iv	interventral	soc	supraorbital sensory canal

Sop	subopercular	B.M.N.H.	British Museum (Natural
sps	spiracular notch		History), London
Ssc	suprascapular	R.S.M.	The Royal Scottish Museum, Edinburgh
A.M.N.H.	American Museum of Natural History, New York	U.M.Z.C.	University Museum of Zoology, Cambridge.